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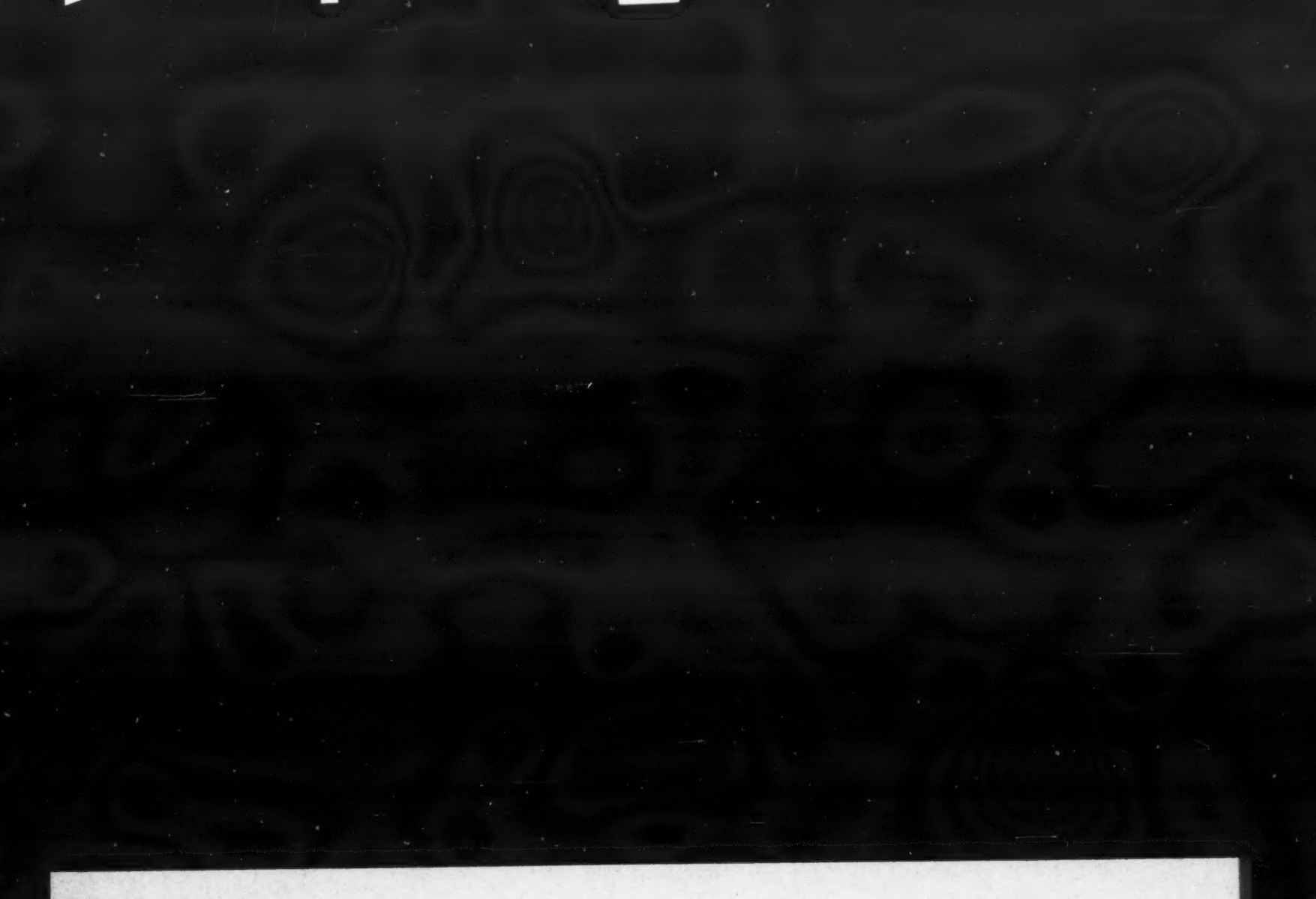

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OÖSPORE GERMINATION IN ALBUGO CANDIDA[1]

T. C. VANTERPOOL

Abstract

In addition to the well-known sessile vesicular zoosporangial type of oöspore germination in *Albugo candida* (Lév.) Kuntze, a second type is described. This consists of an exit tube one to two and a half times the length of the diameter of the oöspore and about one quarter of its width, at the end of which the vesicular zoosporangium is produced. Best results were secured by soaking the oöspores for 7 to 10 days in water at 10° to 12° C and then changing to fresh water. The oöspore material came from hypertrophied inflorescences of rape (*Brassica napus* L. var. *annua* Koch).

Introduction

Virtually every mycologist and plant pathologist is acquainted with de Bary's (1) illustration of the germination of the oöspore of *Albugo candida* (Lév.) Kuntze. It was published in 1863 and has appeared in numerous textbooks and monographs ever since. In this method the epispore ruptures and the protoplasmic contents push out the endospore as a sessile vesicle in which zoospores are formed and from which they escape by rupturing the thin evanescent membrane (Figs. 1 to 3). No other investigation on oöspore germination in this fungus has been reported.

This paper records a second type of germination in which the oöspore first gives rise to a short exit or discharge tube at the end of which a vesicular zoosporangium forms (Figs. 4 to 6 and 13 to 16). The sessile type of germination was, however, more common than the discharge tube type under the conditions described here.

The characteristic brown verrucose and sinuous-ridged oöspores of *Albugo candida* are formed in abundance in hypertrophied inflorescences of rape (*Brassica napus* L. var. *annua* Koch) in the moister areas of the northern part of the crop-growing area of Saskatchewan. Whereas a rape crop following fallow or cereals will show slight infections of *Albugo* or none at all, a rape crop following rape will frequently show 1 to 5% infection (hypertrophies), with an occasional field running as high as 15 to 20%. This suggested that, in nature, the oöspores were serving effectively as a primary source of inoculum. Bearing this in mind and also the fact that the oöspores of many species in the Peronosporales are notoriously difficult to germinate, preliminary attempts were made to germinate the oöspores from rape.

[1]Manuscript received November 7, 1958.
Contribution from the Department of Biology, University of Saskatchewan, Saskatoon, with financial assistance from the Saskatchewan Agricultural Research Foundation.

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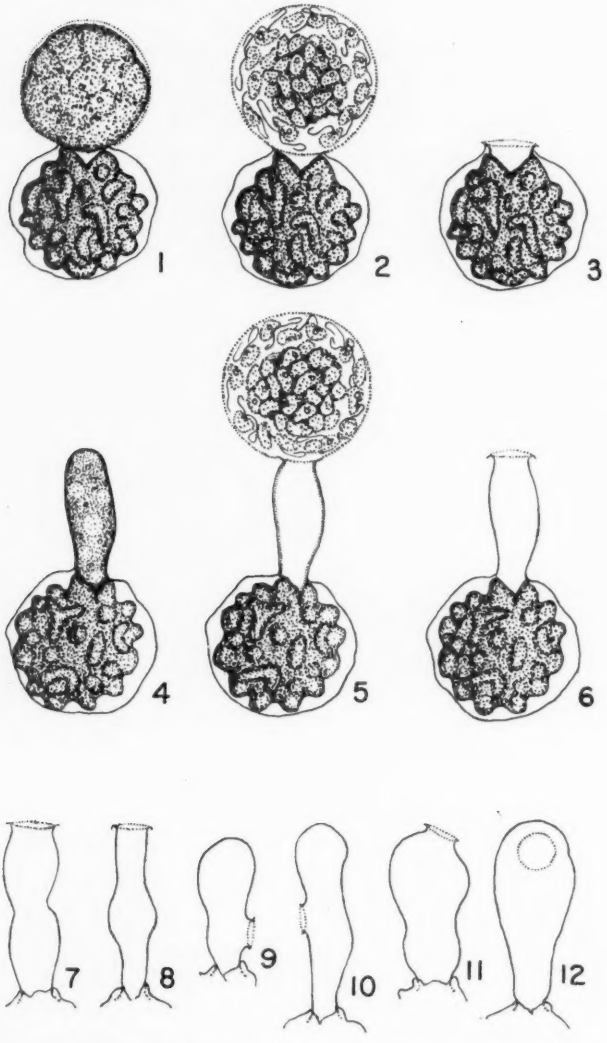
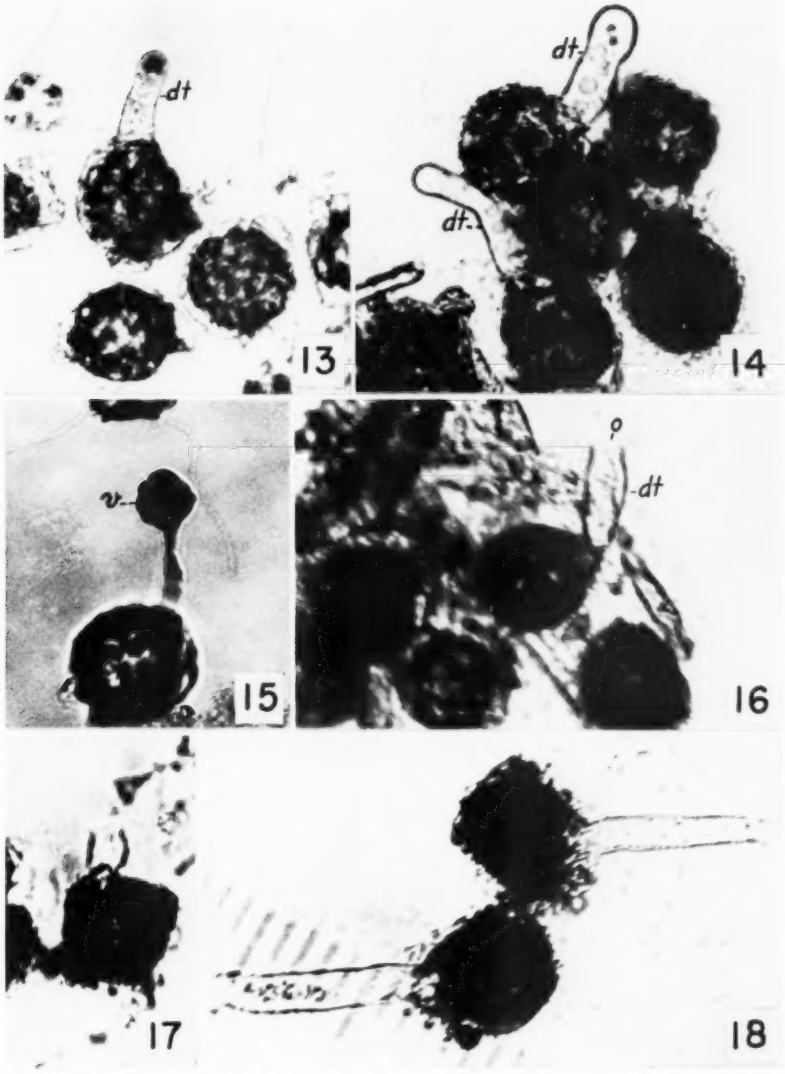


Oöspore germination in *Albugo candida*. FIGS. 1 to 3. The ordinary type of germination with a sessile, vesicular type of terminal zoosporangium. FIG. 1. Shortly after the oöspore contents have been extruded into the vesicle; zoospore differentiation is just beginning. FIG. 2. Shortly before the distended vesicular membrane is ruptured by the active zoospores. FIG. 3. After the zoospores have dispersed. The evanescent vesicular membrane has disappeared, but its attachment to the oöspore is visible as an outward rolled collar. FIGS. 4 to 6. Germination by means of a discharge tube with a terminal vesicular zoosporangium. The wall of the tube, unlike the vesicular membrane, persists after zoospore discharge. FIGS. 7 to 12. The remains of variant types of discharge tubes. In Figs. 9 and 10, vesicle formation was lateral.



Photomicrographs of oöspore germination in *Albugo candida* by a discharge tube and vesicle. FIGS. 13 and 14. Discharge tubes at *dt*, before the contents of the oöspore have passed into a vesicle. FIG. 15. An oöspore stained in lactophenol carbol fuchsin, before its protoplasmic contents had completely passed into the vesicle. The halo-like gelatinous vesicular membrane, *v*, is clearly visible. The contents of the tube and vesicle are shrunken by the lactophenol. FIG. 16. An empty discharge tube, *dt*, with a terminal circular orifice at *o*. FIG. 17 shows one, and FIG. 18 shows two, empty discharge tubes.

Methods and Results

Oöspore material that had been kept in a refrigerator for about 21 months was ground up, sprinkled lightly on the surface of a layer of sterile distilled or sterile tap water 0.5 to 1.0 mm deep in the bottom of Syracuse watch glasses. These were stacked and placed in a refrigerator at 10° to 12° C. The water was carefully drained off or pipetted off with a fine pipette and fresh cool water added frequently during the first few days; later water changes were made once a day. Usually no germination was observed for 7 to 10 days and then in a few of the dishes a trace to occasionally 1 to 4% germination was obtained. This was mainly of the sessile vesicular type as described by de Bary (Figs. 1 to 3), but the exit tube, terminal vesicular type, so characteristic of the zoosporangial discharge in the genus *Pythium*, was quite common, being often as high as a third to a half of those germinating (Figs. 4 to 6). Since empty discharge tubes persisted and could easily be detected, the erroneous impression might be gained that this method of germination was relatively more common than was actually the case. Because of the thick-walled, brown warty epispore and the empty oögonial shell, it was difficult to detect, with certainty, oöspores which had discharged their contents by the sessile vesicular method. Also, in these, it was usually difficult to distinguish between the remains of the vesicular collar (Fig. 3) and the remains of the antheridium which might still be attached to the old oögonial case.

Preliminary attempts to date to increase the percentage of germination, such as alternate freezing and thawing, alternate wetting and drying; temperature variations, light variations; the additions of bits of leaf or flower material of the rape plant, of soil extract, or of oxidizing agents; and the burying of the oöspore material in moist soil for a few weeks, have lead to no improvement. Germination was always irregular and uncertain.

In those cases where discharge of the oöspore contents was observed, whether of the sessile vesicular or terminal vesicular type, zoospore differentiation either had not begun or was in its very early stages. In the discharge shown in the photomicrograph in Fig. 15, the flow of the protoplasmic contents of the oöspore through the exit tube into the vesicle showed no definite signs of zoospore differentiation up to the time the lactophenol solution was added. It was estimated that there were from 40 to 60 zoospores in those cases in which zoospore escape from the vesicles was observed. In comparison, it is interesting to note that on germination the conidia of this fungus commonly extrude their contents into a sessile vesicle in a more advanced stage of zoospore differentiation. The conidia give rise to 4 to 12 zoospores.

Exit tubes varied in length from one to two and a half times the diameter of the oöspores (45 to 125 μ) and 10 to 18 μ in width. The progress of discharge through tubes was observed only three times, but vesicle maturation was observed over a score of times. The conditions favoring discharge appear to be restricted. Numerous tubes which failed to function were observed day after day. Several tubes about twice the usual length with a slight

constriction near the middle were observed (Fig. 7). Discharge through one of these was seen. It is possible that with the intermittent examinations of the cultures, normal discharge was interfered with and that when the culture was replaced in the refrigerator, the tube continued to grow. At no time, however, was there any indication that the tube developed into a mycelium or a germ tube capable of effecting direct penetration of the host plant. Neither was a conidium ever observed at the end of an oöspore exit tube. The less common types of exit tubes (Figs. 7 to 12) can probably be accounted for by the repeated water changes, perhaps sometimes following staling conditions, and removal for microscopic examination when higher temperature and varied light conditions would be encountered.

Actively swimming zoospores were frequently observed inside oöspores and often remained active for as long as 3 hours when kept at about 12° C, but their escape was never seen though they were kept under long observation. This suggested a third type of germination in which complete maturation of the zoospores, followed by direct escape through the ruptured epispore wall, occurred within the oöspore. That this is probably not the case was suggested by two observations: (i) the active zoospores within the oöspore appear to be less than the full complement of 50 or more, and (ii) in two instances of zoospore escape, one by the tube method, about three quarters of the zoospores escaped through the vesicular membrane, while the remainder were entrapped within the oöspore where they continued their activity for about 15 minutes, when observations were terminated. It was not determined whether some of the zoospores completed their maturation within the oöspore and some in the vesicle, or whether all matured in the vesicle and, at the time of dispersal, re-entered the oöspore.

The exit tube, terminal vesicular zoosporangial type of oöspore germination in *Albugo candida*, and the sessile vesicular type in the oöspore of *Peronospora tabacina* as reported by Person and Lucas (2), re-emphasize how closely environmental conditions influence the type of germination in the Peronosporales and also the close relationship of various members of this order.

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1. De Bary, A. Recherches sur le développement de quelques champignons parasites. Ann. sci. nat. Botan. (4 sér.), **20**, 5–148 (1863).
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BIOSYSTEMATIC STUDIES ON XANTHIUM: TAXONOMIC APPRAISAL AND ECOLOGICAL STATUS[1]

DORIS LÖVE AND PIERRE DANSEREAU[2]

Abstract

The following paper is an evaluation of the taxonomic and ecological status of the genus *Xanthium* L. A review of its systematics demonstrates that many so-called "species" described on material from Europe actually have their origin in America, except one, *X. strumarium* s. str., which seems to have a Mediterranean–European center of dispersal. Another conclusion drawn is that *Xanthium* consists of only two distinct species: *X. spinosum* L. and *X. strumarium* L. The former is a relatively stable species, the latter an enormously variable one readily subdivided into a number of minor taxonomic entities.

Ecologically, in eastern North America at least, *Xanthium* is primarily a beach plant, which prefers open habitats and succumbs to crowding. The seeds are most often dispersed by water and wind. It enters easily into ruderal habitats, but only as long as these are open and unshaded.

The generalized short-day flowering response in this genus supports our hypothesis that *Xanthium* has a tropical–subtropical origin, and we feel that it has its center in Central and/or South America, whence it has spread over the continents north and southward.

There is no evidence for any sterility barriers separating the entities of *X. strumarium*, but we feel that an intense inbreeding with an occasional outbreeding is responsible for the enormous variation, often resulting in small, local, but unstable taxa.

The genus *Xanthium* lends itself extremely well to a detailed biosystematic study, if by this we imply an application of the technique and theories of all biological disciplines to the elucidation of taxonomic complexes. As a matter of fact *Xanthium* taxa are very confused at the present time; their geographic distribution is perforce poorly drawn; some of their physiological responses, on the other hand (especially photoperiodism), have come to be well known; their cytogenetic behavior probably is quite simple but has not been explored; and finally their ecological limitations have barely been sketched.

It has therefore seemed to us very worth while to make a preliminary review of these separate aspects of *Xanthium* (with special emphasis on eastern North American material) and to proceed by means of population sampling in stations for which we can ourselves collect satisfactory biometrical and ecological data. This introductory paper attempts such a review and outlines a framework for extensive studies over a period of years. Perusal of a great quantity of herbarium material and preliminary consideration of our field and laboratory data of 1955–58 allow the formulation of a working hypothesis which we propose to outline herewith. We fully expect the analysis of our mass collections, the greenhouse and laboratory experiments, and the herbarium studies which will follow to cause a shift in our present views. They are therefore offered as tentative.

[1]Manuscript received September 10, 1958.
Contribution from l'Institut Botanique, Université de Montréal, Montreal, Que.
[2]Institut Botanique, Université de Montréal.

The present research was undertaken as part of the Biosystematics Programme sponsored by the National Research Council of Canada at the Institut Botanique de l'Université de Montréal. We also wish to acknowledge the collaboration of Áskell Löve (Université de Montréal) and Hubert Vogelmann (University of Vermont), who participated in the field work, and of Jenö Arros, Lascelles Nadeau, and Françoise McNichols, who helped in the biometrics and illustration.

Taxonomic Review

An old Swedish proverb says: "A beloved child has many names," and if we should judge from the amount of species names bestowed on the various forms within the genus *Xanthium*, this seems indeed to be one of the most beloved genera of botany. In American floras and handbooks during the last 100 years it is possible to find some 50 different specific epithets, of which about 20 are widely used (cf. Tables I and II). Still the taxonomists continue to argue: do we or do we not have more than one real, though admittedly quite variable, species? It has hardly been possible to reach a consensus regarding the correct name of this species, and there is little agreement as to its origin, as botanists from all continents seem to regard its existence in their area as an unwanted introduction from somewhere else.

In his "Species Plantarum" Linnaeus (30) described two species, *Xanthium strumarium*, whose stems are unarmed, and *X. spinosum*, whose stems are armed with spines at the nodes. The latter is fairly constant, easily recognizable, and has caused hardly any confusion throughout its almost world-wide distribution area. De Candolle (19) placed it in the distinct section *Acanthoxanthium*. It will therefore be totally left out of our discussion, and when *Xanthium* hereafter is mentioned in a general way we shall refer solely to the one (or more) species of the section *Xanthium* (= *Euxanthium* DC.). It is in this section that confusion now reigns.

X. STRUMARIUM and X. ORIENTALE

Linnaeus himself, in 1753 (30), must have sensed that his species, *X. strumarium*, was not uniform, and that there might be a difference between European and American specimens, as he introduced under *X. strumarium* a *β Xanthium elatius & majus americanum* under which he also included a reference to *X. majus canadense*. But he gave "*Europa, Canada, Virginia, Jamaica, Zeylona, Japonica*" as the area for all three forms.

However, in the third edition of his "Species Plantarum," in 1764 (31), Linnaeus split up *X. strumarium* into *X. strumarium* ("*habitat in Europa*") and *X. orientale* ("*habitat in China, Zeylona, Japonica*"). Under *X. orientale* he then included references to the larger and more robust American and Canadian plants, but did not seem quite content with the fit of the American plants under this name. He described *X. orientale* in the following manner:

"Facies X. strumarii sed planta majus scabra: Folia ovata basi cuneata, obsolete triloba s. quinqueloba, serrata, trinervis; minime vero cordata aut trinervata. Fructus triplo majores et longiores, apicibus duobus distantibus et uncinatis, uti reliqui fructus aculei, basique

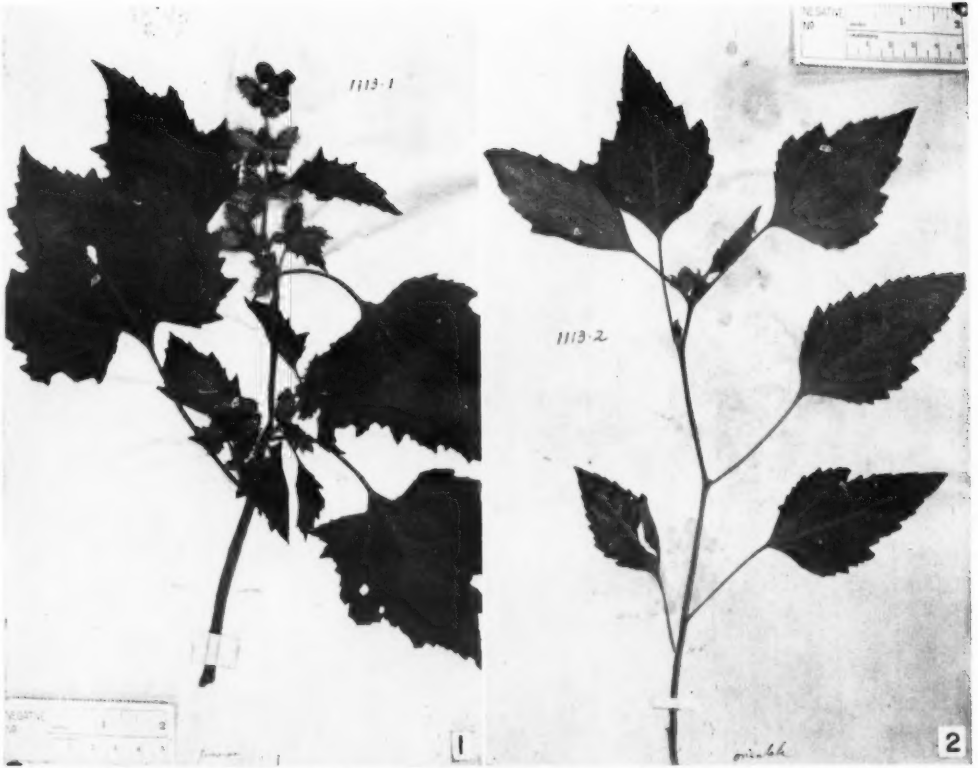


FIG. 1. *Xanthium strumarium* from the Linnean Herbarium (photostat courtesy of the Linnean Society of London).
FIG. 2. *Xanthium orientale* from the Linnean Herbarium (photostat courtesy of the Linnean Society of London).

pubescentes. Flores masculi paleis flosculo duplo longioribus, recurvatis. Bracteae lineares, integerrimae adstant fructibus, solitares s. binae, quae non sunt in priore. Synonyma americanae planta an differant?"

("Has the appearance of *X. strumarium*, but is a more scabrous plant: The ovate leaves have a cuneate base, are indistinctly three- to five-lobed, saw-toothed and three-nerved; less often really cordate or three-nervate. The fruits are three times bigger and longer, with two distant but hooked tips, which like the other spines of the fruit, also have hairy bases. The palea under the male flowers is twice as long as the group of flowers and recurved. The linear bracts are quite entire, close under the fruits, single or in twos, as is never found in the first-mentioned. Does the synonymous American plant differ from this?")

From the Linnean Herbarium in London we have obtained pictures of Linnaeus' specimens of *X. strumarium* and *X. orientale*. The *strumarium* specimen (Fig. 1) is of a fully grown plant with mature fruits, showing quite distinctly their straight, pointed beaks. The *orientale* specimen (Fig. 2), on the contrary, is a poorly developed young plant with immature fruits. For the description of this species Linnaeus must have used mature fruits as well, judging from his own words, but from the picture of his specimen we do not get the impression of his concept of *orientale*.

We must, however, bear in mind that the specimens stored in the Linnean Herbarium in London do not represent a Linnean type collection. Linnaeus did not have the type concept, an invention of latter days, and his herbarium does not always contain the very plants on which he based his species description (24, 28). In using Linnaeus' London Herbarium we must therefore remember that although these specimens have actually been handled by Linnaeus, they are not necessarily in all cases type specimens! The historical value of this collection is far greater than its taxonomic importance.

Miller, in 1768 (33), described in his "Gardener's Dictionary" what he called *Xanthium canadense*, which he made synonymous with Linnaeus' *X. orientale*. Linnaeus had based his descriptions mainly on the leaf shapes, which in *strumarium* are "*cordatis, trinervatis*" (cordate, three-nerved), but in *orientale* are "*cuneati-ovati, obsolete tri-quinquelobati*" (cuneate-ovate, indistinctly three- to five-lobed), and on the size of the fruit. Miller made the same distinctions between *strumarium* and *canadense*, and he also stressed the characteristics of the fruit of *canadense*, which he said was much bigger and with stronger and more bent spines than that of *strumarium*. Further, he found that *strumarium*, which he considered native to Europe, flowered in July and produced ripe seeds, whereas *canadense*, which he assumed to be a native of North America, flowered in August and produced ripe seeds in England only when the fall was long and warm, a fact which supports the assumption that it was a plant introduced from a warmer climate. It seems fairly evident that *canadense* Mill. and *orientale* L. are identical. Miller's contribution was to locate its area correctly.

X. CHINENSE

In addition to his *strumarium* and *canadense*, Miller (33) also described a third *Xanthium*, which he called *chinense*, believing that it originated in China. But later (34) he corrected this and stated that his type came from Vera Cruz, Mexico. This plant, according to Miller (33), much resembles *X. strumarium* in size of the fruit, but the spines are more slender, longer,

and straighter. In England it flowers in July–August, but the fruits rarely if ever ripen. To germinate seeds and to keep the seedlings growing, additional heat has to be provided. It is thus evidently a plant introduced from a much warmer climate, i.e. subtropical North America.

Miller did not mention anything about the hairiness of his *chinense* fruits. The first clear reference in the literature to a *Xanthium* with a pubescent fruit was made by De Candolle in 1815 (18), when he described *X. macrocarpum*, and to a *Xanthium* with a glabrous fruit, also by De Candolle, in 1836 (19), when publishing *X. macrocarpum* β *glabratum*. De Candolle cultivated two kinds of American *Xanthium* in the Paris Botanical Garden. One of them, *X. macrocarpum*, was, according to De Candolle himself (18), a synonym of *X. orientale* L., and the other was the glabrous-fruited type referred to above. Later investigators seem to agree completely that this *macrocarpum* β *glabratum* is synonymous to Miller's *chinense*, and has nothing to do with *X. orientale* L. at all. If we further consider *X. occidentale* Bertol. (1), and *X. longirostre* Wallr. as well as *X. pungens* Wallr. (35, 46, 47) as later synonyms for Miller's *chinense*, we find that this type is fairly widely distributed in the West Indies as well as on the mainland in the southeastern United States. In this latter area it meets and crosses with other *Xanthium* types from the mainland (35).

X. ECHINATUM

Murray's description of *X. echinatum* in 1784 (37) is very clear, and his plants came from seeds collected by von Wangheim at New York, leaving no doubt that they were of American origin. The most distinctive feature of the species is the fruit:

"Capsula ovalis, olivae magnitudinis, hirsuta, antice hamosa, hamis inflexis hispidis, vestita aculeis uncinatis, divergentibus, confertis, sursum et apice nudis, basi deorsum echinatis per setas rigidas albidas, rectiores; bilocularis."

("Capsule oval, the size of an olive, hirsute; at the tip with claws, which are hooked and hairy; clad in bent, divergent, closely standing spines, which are naked towards and at the tip, but at the base are hairy with stiff, straight, whitish hairs; bilocular.")

Murray continues and compares his new species with *X. orientale* L. in the following manner:

"Collatis Xanthio echinato cum X. orientale L. hoc ipsum definiri poterit per Xanthium caule inermi, fructo cylindrico-ovato aculeato: Aculeis uncinatis rarioribus basi pilosis. Sed differt hoc etiam aculeis magis incurvis, macularum in caule defectu, foliis minus manifeste trilobis. . . ."

("When comparing *X. echinatum* with *X. orientale* L. the latter can be defined as a *Xanthium* with an unarmed stem, and a cylindrical-ovate fruit with spines; the spines are few, hooked and hairy at the base. It also differs by having more hooked spines, in lack of spots on the stem, and less obviously trilobate leaves.")

There seems thus little reason to confuse *echinatum* Murr. and *orientale* L. as Wallroth (46) did in his description of *echinatum*, when he referred to its shiny, short-glandular fruit with strong, hooked, sparse ("entfernt stehenden") spines and a very crooked beak. As synonyms he gives for instance *X. macrocarpum* DC. and the pre-Linnean *X. canadense major* Tourn., both of which we now know are identical with *X. orientale* L. (19, 44). Unfortunately Wallroth's confusion leaves us somewhat uncertain as to which type it was

that Lagasca (29) collected around Madrid, Spain, in 1811, as well as to the type later collected by Mademoiselle Dunal in Languedoc, France. It seems, though, that both these collections were of the *orientale*, not the *echinatum*, type (29, 43).

X. ITALICUM

Still another *Xanthium* type described from Europe is of interest to us, namely *X. italicum*. The name was first published by Moretti in 1822 (36), who based his description on plants found growing along the River Po from Turin to Padua and around Porto di Termo, a small harbor on the coast of Abruzzi, Italy. The type seems close to Murray's *echinatum* and was first identified as such by Moretti himself (35). The main difference between the two types lies in the size of the fruit, which is smaller in *italicum*, but especially in the shape of the beak, which in *echinatum* is very hooked, in *italicum* more protruding, usually only curved and sometimes almost straight, and definitely more slender than in *echinatum*.

Even if Moretti (36) did not say so, it seems to us that the *italicum* type is more likely an introduced or naturalized species than an indigenous one in Italy. When Moretti described it, it was common in the Po Valley, where it seems to have found ideal habitats along the river beaches. It may have entered at some port in the Po delta, and spread up the system of rivers and canals towards the interior. On the other hand, it was apparently very local around the small harbor of Porto di Termo, where there is no river to take it inland into the Apennine Mountains, and thus it remained isolated. Now, *italicum* is a fairly common *Xanthium* type all over southern Europe, but in North America it is also one of the most widely spread types over the continent. It is also found in Hawaii (35) and probably elsewhere. We do not think it improbable that its true homeland is North America, not Italy.

X. CAVANILLESII

Millspaugh and Sherff (35), in their monograph of the North American *Xanthium*, kept *italicum* and *echinatum* distinct, but were not sure of the relationship between *X. italicum* and *X. Cavanillesii* Schouw. The latter was first described by the Danish botanist Schouw in a seed list from Copenhagen (39). His material originated from Buenos Aires, collected by Didrichsen. Schouw's description of the fruit is clear:

"Involucre fructigero ovali, inter aculeos et ad basin rostrorum hispidissimo; aculeis teniter subulatis, strictis, inferioribus retrorsum porrectis; rostris tenuibus, strictis, apice uncinatis.'
("The fruiting involucre oval, very hairy between the spines and at the base of the beak; the spines are slightly awl-shaped, straight, the lowermost retrorsely bent outwards; the beak is narrow, straight, slightly bent at the tip.")

It seems that Millspaugh and Sherff (35) had not seen material of *Xanthium* from Brazil, which can be clearly referred to Schouw's type. Moreover, *X. Cavanillesii* seems to be the only definitely indigenous type of this kind in Brazil as well as in other parts of South America, both along rivers and on cultivated land in subtropical, tropical, and warm-temperate areas reaching as far north as Mexico. In the Old World, the *Cavanillesii* type is today met

with in Spain and North Africa as a weed, and also in South Africa in the sheep-grazing areas. If Millspaugh and Sherff (35) had been familiar with the Brazilian plants, they would obviously not have described their new species *X. australe*, which as Widder (47) also points out in 1923, is practically identical with *X. Cavanillesii*. The illustrations in Millspaugh and Sherff as compared with those of Widder bear this out quite clearly. Widder is, however, of the opinion that *X. Cavanillesii* may be the type from which certain North American *Xanthium* derive, e.g. the west coast type *californicum* Greene and the east coast type *saccharatum* Wallr. This hypothesis will be discussed at a later stage of our work. By and large we agree with it.

X. PENSYLVANICUM

When dealing with *X. orientale*, *chinense*, *echinatum*, and *italicum* the principal monographers of this genus, Millspaugh and Sherff in America and Widder in Europe, agree almost completely. They wrote their papers independently during the First World War, but Widder was able to include an addendum to his paper in 1923 (47) in which he scrutinizes Millspaugh and Sherff (35) and discusses their taxonomical interpretations. He can thus identify *X. australe* M. & S. with *X. Cavanillesii* Schouw. But when it comes to the group of plants which Widder regarded as developing out from the *Cavanillesii* type and which will be referred to below as the *pensylvanicum* type, the monographers dissent drastically.

The discrepancy seems to stem from the different interpretations of Wallroth's monograph of *Xanthium* (46), in which he described among others three species, *X. pungens*, *X. pensylvanicum*, and *X. saccharatum*. Millspaugh and Sherff (35) regard *saccharatum* and *pensylvanicum* as synonyms and use the latter name; *pungens* is, according to them, synonymous with *X. chinense* Mill. Widder (47) regards *pensylvanicum* as a synonym for *pungens*, and sees in *saccharatum* (especially in the Addendum) a very large collective type distributed over most of North America and including a variety of types described under several names by Wallroth (46), Millspaugh and Sherff (35), and Greene (25).

Wallroth's *pungens* was described from a plant that was found growing on the city dump of Nordhausen (Saxony, Germany). The seed, from which it came, had been attached to the tail of a raccoon skin, obviously thus of American origin, as raccoons do not occur in Europe. As synonyms Wallroth gives among others *X. macrocarpum β glabratum* DC. (which we now consider equal to *chinense* Mill.) and "*X. car. medium fructu toroso*" Dill., which is illustrated in Dillenius' "Hortus Elthamensis" (21). Studying Dillenius' picture and text (21), we have, however, arrived at the conclusion that his plant was an intermediate between *X. orientale* L. (= *canadense major* Tourn.) and *X. strumarium* L. (= *vulgare* Tourn.) as is inferred by his words on page 433 in his book:

> "Verbo, inter illam et hanc, vulgarem nempe Canadensem, media est haec species."
> ("Thus, this species is intermediate between *vulgare* and *canadense*.")

The illustration also clearly depicts what Dillenius regarded as "*vulgare*" and "*canadense*," and these are no doubt the same as *strumarium* L. and *orientale* L. The description given by Wallroth for *X. pungens* (46) does not fit Dillenius' picture very well, but agrees better with the accepted type of *chinense* Mill. (= *X. macrocarpum* β *glabratum* DC.). We think, therefore, that Widder (47) made a mistake, when he considered *X. pungens* Wallr. as a synonym of *pensylvanicum* Wallr. instead of *chinense* Mill., but that the area Widder designated for "*pungens*"—from the plains to the mountains in eastern North America from Ontario – Missouri – Kansas – east Texas to the Atlantic Coast—is roughly the same as the mainland distribution of *chinense* Mill.

When Wallroth himself (46) described *X. pensylvanicum* he used two different plants as a basis, one from Asheville (North Carolina), collected by Beyrich, which he called α *glandulosa* due to the presence of glands among the hairs at the basis of the beaks and spines, and another, collected by Poepping in Pennsylvania, which he named β *eglandulosa* because it lacked glands. However, Millspaugh and Sherff (35) have examined the co-type of *eglandulosum* and found it glandular, and thus there is no reason to keep the two varieties apart. Wallroth described his species generally as having elliptic-ovate fruits, golden glandular in color and with slightly bent spines about as long as the beaks. The fruits are also hairy. The description is vague enough to fit most of the types of hairy-fruited *Xanthium* met with in North America, but seems well separated from the glabrous-fruited *chinense* (= *pungens* Wallr.). In *pensylvanicum* Wallr., Millspaugh and Sherff (35) also included Wallroth's *X. saccharatum*, of which they have seen a co-type from "Bexar (?), Texas." They also refer *X. affine*, *californicum*, and *acutum* Greene to the same species complex.

Widder (47) used the name *saccharatum* Wallr. in much the same way as Millspaugh and Sherff used *pensylvanicum*, but tended to widen the concept of the species to include even more variation than the two Americans permit. Wallroth's own description of *X. saccharatum* seems to us fairly limited and reminds us a little in some of its details of *X. Cavanillesii* Schouw, e.g. in the character of the beak, which Wallroth (46) described as:

"kaum dreimals stärker ausgebildete, etwa um die Hälfte längere, elliptische, allmählig zugespitzte, fest und ungleich zusammengeklappte Schnäbel."
("hardly three times as thick, about one half longer than the spines, elliptical, firmly and unevenly compressed beaks.")

The plant is included in the group with very hairy and glandular fruits, which probably puts it close to a *Cavanillesii* type. It seems to us, therefore, that Widder has chosen a less suitable name from Wallroth, but that if we make *pensylvanicum* and *saccharatum* synonyms we subscribe to Widder's discussion (46) of this taxon.

Our own *pensylvanicum* complex is thus very wide. It ranges practically all over North America, varies enormously, has the strongest affinities to *italicum* (which is also heterogenic), but is also related to other groups like *echinatum*, *Cavanillesii*, and *chinense*.

X. OVIFORME

Widder (47) suggested that several of Millspaugh and Sherff's new species (e.g. *Wootoni* Cock., *leptocarpum* M. & S., *cenchroides* M. & S.) be included as "mutants" of *saccharatum* (= our *pensylvanicum*) as he understands it. He regarded the illustrations of Millspaugh and Sherff's *italicum*, *pensylvanicum*, *oviforme*, and *campestre* only as forms and variations of his "*saccharatum*." However, among these latter taxa, *oviforme*, described by Wallroth in 1844 (46), seems to us a rather distinct type with its immense burs, coarse spines, and very large, hooked beaks. Millspaugh and Sherff (35) claim that it is distinct from Greene's *campestre* (25), because of a ventral groove in the *oviforme* spines, which would be lacking in *campestre*. We have observed a number of plants in the states of Washington and Oregon with burs otherwise typical of *oviforme*, but failed to find the ventral groove as a constant feature. Therefore although we regard *oviforme* as distinct from *pensylvanicum* we can recognize *X. campestre* Greene only as a synonym of *X. oviforme* Wallr.

The *oviforme* complex is at home in Washington, Oregon, and California in the dry interior, but has also been found as a weed in Illinois (35), and according to Fernald (23) from southern Quebec across to Michigan and south to Pennsylvania. It seems to us, from studies of herbarium material, that *oviforme* on the east side of the continent is more variable and shows distinct signs of intergradation with other big-fruited types of *Xanthium* like *italicum* (23), as well as *echinatum*, *pensylvanicum*, etc. This is probably the reason why Widder (46) looked upon *oviforme* only as a "mutant" of his *saccharatum* (= *pensylvanicum*). On the west side of the continent, however, it seems to us that it is easier to see a continuation from the South American – Mexican *Cavanillesii* group towards the more northern *oviforme* complex.

Other Types

Widder (46) thought he could see a relationship between *X. curvescens* M. & S. and his concept of *X. pungens* Wallr. (i.e. = *chinense* Mill. from the mainland), which he claimed had its parallel in a relationship between *X. occidentale* Bertol. (i.e. = *chinense* Mill. from the West Indies) and *X. orientale* L. It is more astonishing that he failed to see the close relationship between *orientale–curvescens–leptocarpum* and *Wootoni* around Lake Champlain in Vermont. Probably he lacked sufficient material from this interesting and critical locality.

We cannot avoid the impression that Widder's concepts of the delimitation of the *Xanthium* taxa changed as he wrote his Addendum. He even became uncertain regarding "species" like *echinatum* and *italicum*, which he had defined so sharply in the first part of his paper.

Revisional Trends

It seems that a sort of saturation point in *Xanthium* taxonomy had been reached with the paper by Millspaugh and Sherff (35), for the problem had become so intricate that it must lead either to a still more intense splitting of

species groups until a *Taraxacum*-like situation is reached, or else to a unification of the smaller entities into larger or even very large groups (45). In the first case, practically every local collection would represent a seemingly "good" species; in the latter case, the extreme variation and intermediate forms between such local groups must be discounted as minor variations not deserving of nomenclatorial recognition. It is fairly evident that as long as "species" based on plants obviously introduced from America were described from Europe, they seemed relatively simple and uncomplicated, but when the rich source from which they all came began to be explored, the problem of species delimitation soon became so involved that it got out of hand.

It cannot be denied that Millspaugh and Sherff's paper (35) on the North American *Xanthium* is the most valuable and critical produced in this field up to date, and the criticism and alterations given it by Fernald (22, 23) seem to us unwarranted. Fernald (23) constructed a new key to the genus in Gray's Manual, somewhat reduced the number of species, and made alterations in the synonymy, but unfortunately he did not improve our understanding of this difficult genus. His key is useless even as a means of identifying the taxa of *Xanthium*. In this respect the Millspaugh and Sherff key (35) is far superior, and the numbers and measurements given by them are considerably more accurate than the grossly exaggerated figures offered by Fernald. Millspaugh and Sherff's excellent pictures and photographs are also valuable, and their care and caution in naming new species is praiseworthy.

However, the trend to unite rather than to split, as foreshadowed already by Widder (46), was followed up by Wiegand (48), who took the bold step of lumping all previously described American taxa of *Xanthium* (excluding *X. spinosum*) into one large species which he named *X. orientale* L. Still, he realized that his taxon was not uniform and suggested a division into four entities in the following manner:

"1) Burs glabrous or minutely puberulent and atomiferous, fusiform, somewhat smaller than others (*X. chinense* Mill.; *X. pungens* Wallr.; *X. glabratum* Britt.; *X. americanum* Britt. and Brown; *X. canadense* Gray's Manual.).

2) Burs more or less hispid, the body ellipsoidal with prominent beaks (*X. italicum* Mor.; *X. pensylvanicum* Wallr.; *X. commune* Britt.; *X. canadense* var. *echinatum* pro parte Cayuga Fl.).

3) Burs hispid, the body ovoid, broadly elliptic-ovoid or oval, the beaks less prominent (*X. glanduliferum* Greene?; *X. canadense* var. pro parte Cayuga Fl.; *X. echinatum* Gray's Man.).

4) Spines far apart and few in number, otherwise generally as in nr 2 (*X. Wootoni* Cockll.). The spines in this last-named form vary in number toward the normal and the plants occur as individuals in otherwise normal colonies.

In each of the above-mentioned forms the spines vary greatly in shape and number." (48).

Cronquist (6), severely criticized by Fernald (22), followed Wiegand (48), but preferred, correctly, to use the collective name *X. strumarium* L. as being the taxonomically oldest one. He also found it possible to divide his species into at least two groups, *X. strumarium* L. var. *glabratum* (DC.) Cronquist* and *X. strumarium* L. var. *canadense* (Mill.) T. & G.† for the (glandular-) pubescent and glabrous (-subglabrous) types respectively (7, 8). He

*In Table V including *X. chinense* Mill.

†In Table V synonymous to *X. strumarium* ssp. *Cavanillesii* var. *Cavanillesii*.

also recognized the true European type of *X. strumarium* L., which he found as a weed in American ports and described as small-fruited with a straight beak, i.e. in conformity with the Linnean picture (Fig. 1), but in opposition to Millspaugh and Sherff's illustration of *strumarium* (35). His American varieties intergrade as the overlap in his descriptions imply.

To illustrate clearly in what state the nomenclature of the American *Xanthium* is found in our floras, two tables have been compiled out of the works of Millspaugh and Sherff (35), Fernald (22, 23), and some 50 other easily available and current floras, handbooks, and floristic lists from the United States and Canada. Table I gives a list of names for which synonyms are not found (ordinarily these taxa have very limited areas). Table II gives in the vertical column the names currently used in floras, and in the horizontal one the various synonyms offered for them in the same floras. Probably a more thorough study would reveal still more names and more synonyms to add to our confusion. The species with many synonyms are often widely distributed.

TABLE I

Names applied to *Xanthium* "species" for which synonyms are not found

Name	Distribution
acerosum Greene	Wisconsin – North Dakota – Nebraska (N.Y.)
arcuatum Millsp. & Sherff	New York, Vermont
australe Millsp. & Sherff	Mexico
calvum Millsp. & Sherff	California
campestre Greene	California
cenchroides Millsp. & Sherff	Texas
Chasei Fern.	Illinois
curvescens Millsp. & Sherff	Vermont
cylindricum Millsp. & Sherff	North Carolina (Vermont)
globosum Shull	Missouri–Kansas
inflexum Mach. & Bush	Illinois–Arkansas
leptocarpum Millsp. & Sherff	Vermont
oviforme Wallr.	Washington–Oregon (New York, Quebec, Vermont)
palustre Greene	California
Wootoni Cockll.	Washington, New Mexico (Massachusetts, Minnesota, Vermont)

Since it is our very purpose to eventually revise the whole taxonomy of *Xanthium* (= *Euxanthium* DC.), we do not want to operate with all these names, but we are bound to use a provisional scheme that will serve to orient this study along physiological, genetical, and ecological lines. Therefore, we have recognized seven units, which we shall refer to henceforth as "complexes." These appear to be revolving points in the total variation pattern. Figure 3 shows a typical fruit of each one of these complexes.

Geographical Distribution

The problem of geographical distribution and migration in species of *Xanthium* hinges upon the physiological, genetical, and ecological adaptations which will be reviewed below.

TABLE II

Names commonly given in floras to *Xanthium* "species," and the synonyms which have been referred to them

Flora names	Synonyms																														
	acutum Greene	*affine* Greene	*americanum* Walt.	*aridum* Greene	*canadense* Mill.	v. *echinatum* Mill.	*chinense* Mill.	*commune* Britt.	*echinatum* Murr.	*glabratum* Britt.	*glanduliferum* Greene	*inflexum* Mach. & Bush	*italicum* Mor.	*longirostre* Wallr.	*Maconnii* Britt.	*macrocarpum* v. *glabratum* (DC.) Br.	*maculatum* Raf.	*occidentale* Britt.	*orientale* L.	*oviforme* Wallr.	*pensylvanicum* Wallr.	*pungens* Wallr.	*saccharatum* Wallr.	*silphiifolium* Greene	*strumarium* L.	v. *canadense* (Mill.)	v. *echinatum* (Murr.)	*varians* Greene	*Wootoni* Cockll.
americanum					x		x												x			x								
canadense Mill.			x						x	x						x			x		x	x			x	x			
v. *echinatum* Mill.									x								x													
chinense Mill.			x		x	x				x		x		x				x	x		x	x			x	x				
commune Britt.					x								x										x				x			
echinatum Murr.						x		x									x								x					
glabratum (DC.) Britt.																									x					
glanduliferum Greene								x															x						x	
italicum Mor.											x				x						x								x	
orientale L.			x		x		x	x	x	x		x	x	x							x	x								x
pensylvanicum Wallr.	x	x	x		x					x													x							
pungens Wallr.			x				x														x	x					x			
saccharatum Wallr.								x					x							x										
speciosum Kearn					x																									
strumarium L.		x	x	x	x											x				x	x			x	x	x	x	x		

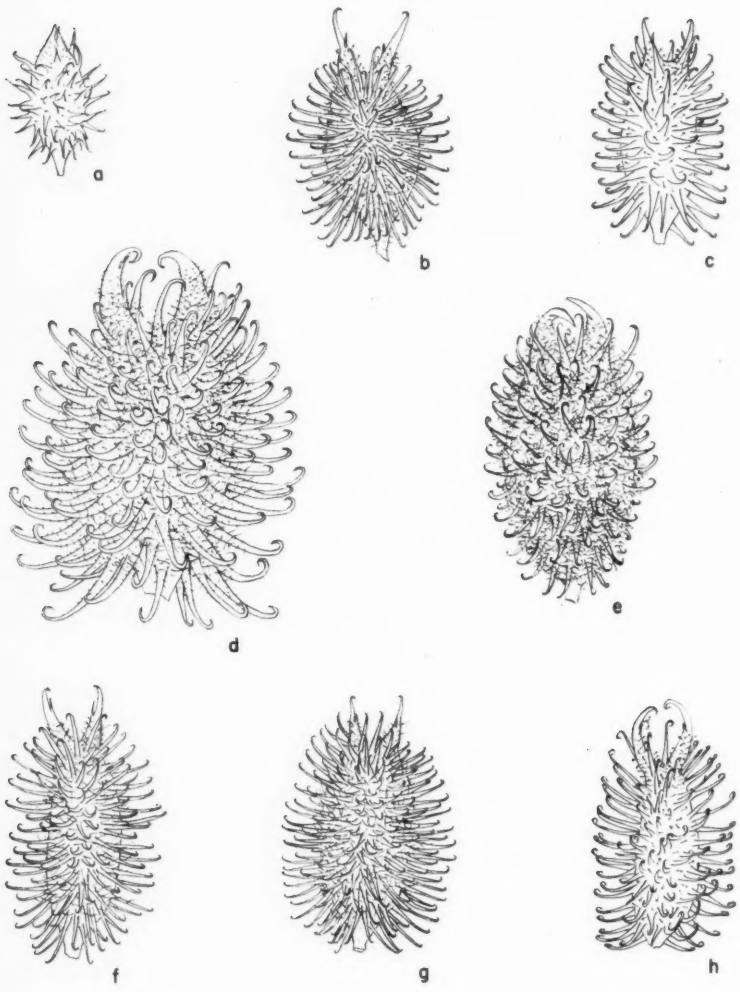


FIG. 3. Typical fruits of *Xanthium* "complexes" as outlined in the present paper (see page 185): *a, strumarium; b, Cavanillesii; c, chinense; d, oviforme; e, echinatum; f, pensylvanicum; g, italicum; h, orientale.* (*a, b, e,* and *h* from fresh specimens; *c, d, f,* and *g* redrawn from Millspaugh and Sherff 1919 (35), Plate VII.)

The best we can do at present is to delineate very broadly the areas of the "complexes" mentioned above:

1. "*Strumarium*" (Fig. 3*a*) is probably the most wide-ranging. It quite possibly has a Mediterranean center of origin around Lat. 30° N. (maybe extending to the deserts of Asia) for only there does it seem to frequent "natural" habitats at all. It was known in this region already in classical times, when the fruits were used as ingredients for a hair dye; hence "*Xanthium*" meaning "yellow" (Dioscorides in Tournefort 1700). Elsewhere it is sporadic and seemingly always in waste places. This is so in Scandinavia where it reaches Lat. 60° N., in the Azores, Mauritius, and Réunion, as well as in east and southeast Asia, where it is spread between Lat. 10° S. and Lat. 40° N. It is also sporadic in North America, and according to Cronquist (7, 8) in tropical America.

2. "*Cavanillesii*" (Fig. 3*b*) is also very widespread, mostly in South America (to Lat. 45° S.) extending northwards to the Gulf of Mexico (to Lat. 30° N.). As a weed it is met with in Spain and North Africa (Lat. 30°–40° N.) and in South Africa (around Lat. 30° S.) in sheep-raising areas.

3. "*Oviforme*" (Fig. 3*d*) shows a narrower range, mostly in the subdeserts of western North America (between Lat. 35° and 48°–?50° N.). It extends as a weed to New England and the Hawaiian Islands.

4. "*Echinatum*" (Fig. 3*e*) has a fairly small range from Quebec over New England down to Virginia (Lat. 35°–45° N.), chiefly on the Atlantic coast, but also inland on sandy river and lake shores. As a weed it has been noted in England and Scandinavia.

5. "*Chinense*" (Fig. 3*c*) is western North Atlantic: including eastern North America and the Antilles, roughly between Lat. 15° and 45° N.

6. "*Hybrid*" is a convenient term for a swarm of related forms among which "*pensylvanicum*" (Fig. 3*f*) and "*italicum*" (Fig. 3*g*) are most frequent. It fairly covers the territory of the United States with little overlap into Canada and Mexico, roughly between Lat. 25° and 49° N. In Europe "*italicum*," most likely from this complex, ranges from the Mediterranean in Italy through west central Europe to the Baltic (Lat. 35°–55° N.). It appeared in Italy around 1800, at the time of early Italian migration to America.

7. "*Orientale*" (Fig. 3*h*) extends over northern Spain and France to the southwest of Germany, Switzerland, and northern Italy (Lat. 42°–50° N.). It was cultivated around Paris in the early 1700's but may also have spread from Atlantic ports up the main rivers. We believe it has connections with *Xanthium* types in the French-populated part of eastern North America.

In the Old World it is thus quite possible that "*strumarium*" is the only true native, and that "*italicum*" and "*orientale*" are introduced from America, but have gained a firm foothold.

Xanthium is also found in Australia and New Zealand as a weed, especially in sheep-grazing areas, but we have not seen any herbarium material from these countries and thus do not know which complexes are represented there.

Generally it appears that *Xanthium* taxa are present between Lat. 45° S. and 50° N. in the western hemisphere and about 30° S. and 60° N. in the eastern hemisphere. Since latitudinal distribution in this genus is in part conditioned by photoperiod, it may be interesting to investigate how far similar lengths of day in North and South America and in western Europe and North America coincide with ombrothermic zones, i.e. with the independent variables of rainfall and temperatures. At the same latitudes western Europe has a milder climate than North America, if by "milder" one considers not only the mean temperature but also the relative moderation of the climate. Thus, Bordeaux and Montreal, at similar latitudes, have respectively a maritime and a strongly continental climate. If, therefore, the lengths of day are likely to influence flowering at the same time, the maturing processes of the seed can be much influenced by extreme late summer heat in eastern North America, whereas the cooler west European temperature may delay it. This seems to be the case in the British Isles and Scandinavia, and the cause for the short persistency of the weedy colonies of *Xanthium* in these areas.

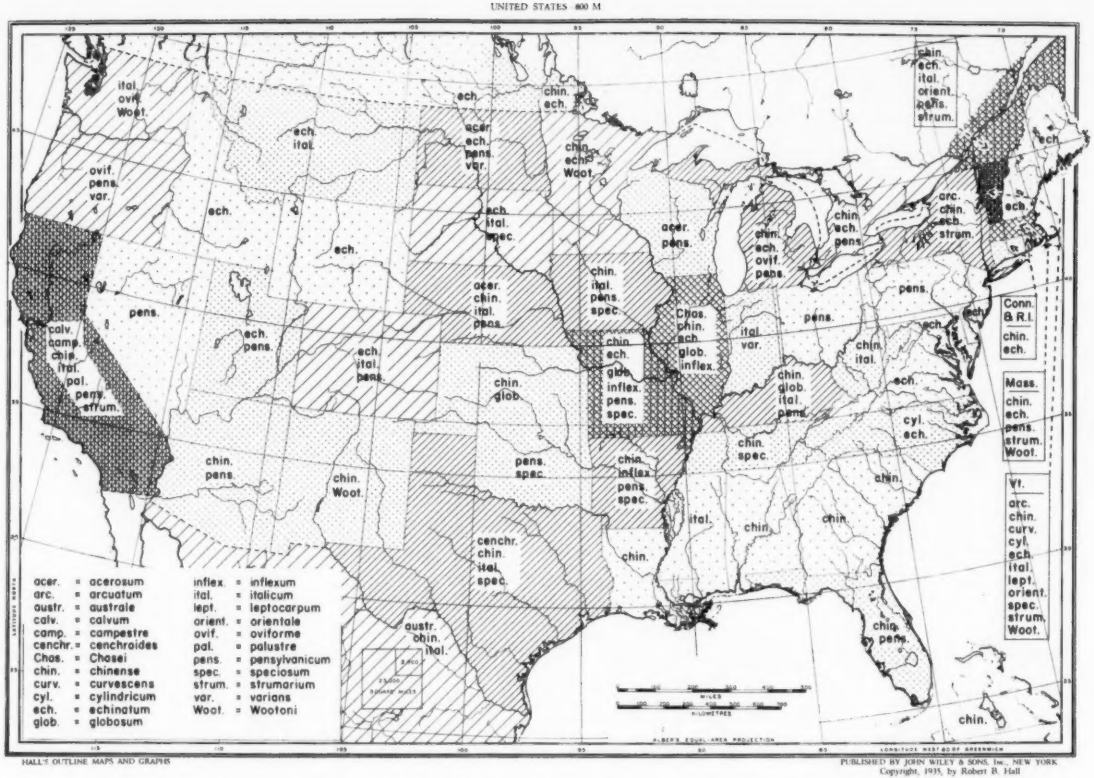


FIG. 4. North American distribution of *Xanthium* taxa. The shading is proportionate to the number of taxa reported from each state or province (a maximum of 11 in Vermont).

As the plants are annuals, one season of no seed production is practically equal to the extinction of the population in question.

In North America, with the possible exception of parts of the southeastern United States and a small strip of the Pacific coast, there are no moderate climates; the strong pulsation of a continental regimen is everywhere felt and is partly attenuated by the Mediterranean influence of the Pacific coast. Much of Central America is subdesert and savannah instead of forest.

Not enough is known of the exact South American, African, and Asiatic portions of *Xanthium* ranges to similarly qualify the climatic conditions under which they live.

Thus, two of our complexes are very wide-ranging, extending to three continents, whereas the other five are merely "regional" (13). The *Cavanillesii* group is primarily tropical, reaching into warm-temperate areas. The *strumarium* complex appears more subtropical and temperate, but extends to include very cold winter areas in southern Siberia as well as tropical areas in southeast Asia.

Among the more limited complexes, *oviforme* is confined to the deserts, halfdeserts, and steppes in the Great Basin of North America, where it encounters very cold and very hot seasons. *Echinatum* is limited to shores and beaches in a similar latitudinal range as *oviforme*, but enjoys a less continental and more maritime type of climate, though still with more marked seasons than parallel ranges in Europe. *Chinense* in the southern part of eastern North America stays essentially clear of temperate grassland and covers mostly beaches in forested areas, although it is found under savannah climates in the West Indies. The *hybrid* complex seems able to withstand any form of climate encountered in the United States of America, but avoids mountainous areas. All the North American complexes have a latitudinal range about 10–15 degrees wide, and reach Lat. 49–50° N.

In Europe the *orientale* and *italicum* (part of the hybrid) complexes are fairly distinct. The former is Atlantic – Mediterranean, the latter central European – Mediterranean. Both are confined within 10–15 degrees latitude, but reach approximately 5 degrees further north (to Lat. 55° N.) than the American plants.

To give a geographical picture of the American *Xanthium* taxa, we have (in Fig. 4) crosshatched states and provinces in relation to the number of *Xanthium* "species" reported for them. Names other than those which we have used for our "complexes" can be regarded as belonging to the "hybrid complex," and they represent the ones used by Millspaugh and Sherff (35) and Fernald (23). It is evident that cockleburs are not very common in mountainous areas; both the eastern and the western mountain regions are rather poor in number of "species". On the other hand, the "species" are both numerous and variable in the lowlands, but especially so where the activities of man are intense, i.e. in New England, in the Middle West, and in California. As seen on the map (Fig. 4) Vermont has the highest number (11) of *Xanthium* "species" according to Millspaugh and Sherff (35) and Fernald

(22, 23). This state is at the crossroads between the St. Lawrence and Hudson river systems, as well as open to the west via the gap in the eastern mountains in the Mohawk Valley, and to the east and the Atlantic seaboard via New Hampshire, Massachusetts, and Connecticut. Human activity in this area has also been strong and gone on for the longest time. In this area practically all our complexes meet, both as indigens and as weeds, including the European *strumarium*, and it has become a veritable melting pot for the formation of new *Xanthium* taxa. Towards the end of this paper we venture to set forth an explanation for this phenomenon.

Ecological Adjustment

Though *Xanthium* is not a bothersome weed in most cases (some weed catalogues do not even include it), it is considered poisonous to pigs and fowl (3, 4, 26), at least in the cotyledon stage. It is common in waste places, on roadsides, on railway banks, on building lots, etc. But it is as often found growing in seemingly natural habitats like moist sandy pits, river banks, dunes along the coast, and around inland marshes, not seldom in rather saline conditions. Generally it avoids congestion and prefers an open vegetation, for it disappears quickly if crowded. Spreading from apparently natural sites, it therefore takes advantage of habitats created by man, and may thus suddenly disperse from an earlier isolated locality over vast areas along roadsides, railway embankments, etc.

The plants are apparently rather tolerant to various soil conditions, ranging from rich-moist to dry-sandy and saline. They produce a great multitude of fruits, which are easily dispersed when the spines attach them to fur and clothing, and also by wind as they are very light, and by water as they float well and can stand a long time in water. When given the right conditions they germinate quickly and easily.

Since it is our purpose in our biosystematic studies to focus the environmental dimensions of the taxa that we are dealing with as sharply as their morphological and genetic make-up, we shall offer some descriptions and interpretations of the habitats wherein they grow, in order to estimate the kind, intensity, and rhythm of environmental factors that exert pressure upon them. No such data are available from most of the literature examined: floras provide only the most generalized statements and no systematic accounts of *Xanthium* habitats are to be found in any ecological monographs that have come to our attention. It may be possible to use ecological studies pertaining to habitats where *Xanthium* is known to grow (e.g. in South Africa, Europe, and indeed in various parts of North America), but the only truly reliable approach, as it seems to us, is direct field observations on *Xanthium* habitats, undertaken for the very purpose of our study. At all events the present paper offers as a point of departure an analysis of the natural environment of *Xanthium* taxa in northeastern America where our material is being observed *in situ*, collected, measured, grown, and experimented with. These descriptions and interpretations as well as the approach and method of field

work largely correspond to the ideas and principles detailed in Dansereau's "Biogeography, an ecological perspective" (16). The present study is also an application of the procedure outlined by Dansereau in 1952 (13): the "varieties of evolutionary opportunity" are conditioned in part by natural selection, which can only be defined in ecological terms.

In the first place, *Xanthium* in eastern North America is a shore plant, more exactly a beach plant. The ecological meaning of the term beach has been discussed at some length elsewhere by Dansereau (10). As shown in Figs. 5–9, it is an area of variable width that extends between open water (summer level) and that part of the embankment which is called the levee.

The zonation of shore vegetation is somewhat variable, since it depends on texture of substratum, slope, duration of flood. In any one region (such

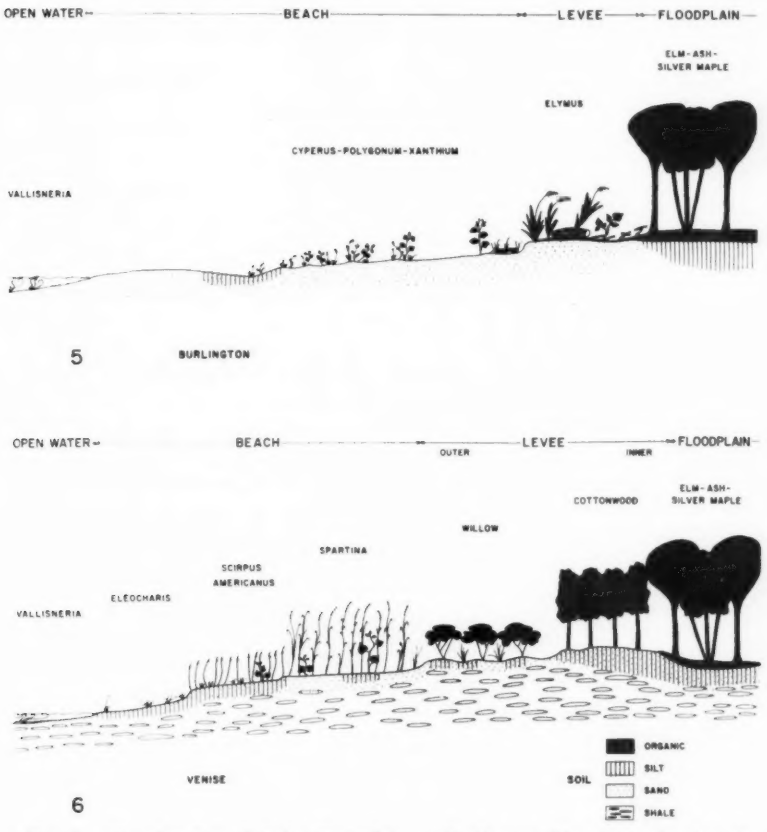
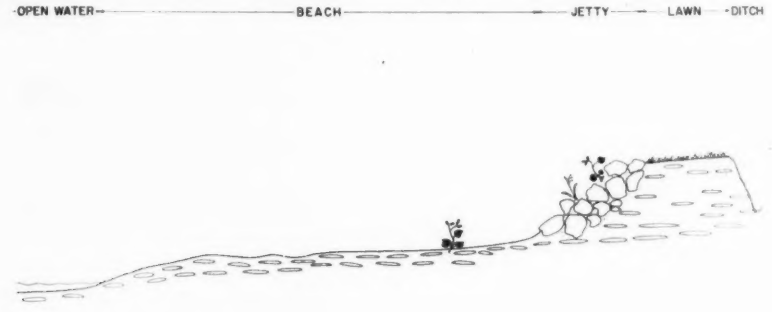


FIG. 5. The shoreline of Lake Champlain at Burlington (Vermont), showing the vegetation belts that lie between the open water and the floodplain forest.

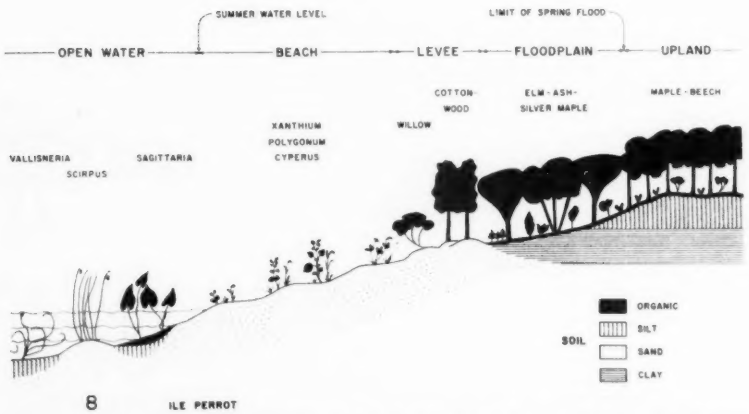
FIG. 6. The shoreline at Venise, Missisquoi Bay (Southern Quebec), showing the vegetation belts between the open water and the floodplain forest.

as the Middle St. Lawrence – Champlain lowlands) the order of the belts of vegetation is constant. On a very long and gradual slope, a full development of the potential zonation can be expected, especially if the substratum shows little change of texture or if the latter is gradually modified. A virtually complete zonation in the St. Lawrence system was illustrated by Dansereau in 1956 (15, Fig. 16) and 1957 (16, Fig. 3.33, p. 166). It was shown that many telescopings of this pattern commonly occurred (15) and that intrusions could be expected in the gradient where an abrupt change took place.

In fact, the ecological process called "cornering" was originally described (14) with special reference to shore zonations. It is of considerable importance, in the case of the annual cockleburs, which must establish new populations each year, to provide some measurement of the opening and closing of the rather narrow ecological gradient in which they are fitted.



7 VENISE



8 ILE PERROT

FIG. 7. A transect similar to that of Fig. 6, where the natural vegetation has been stripped by man.

FIG. 8. The shoreline at Ile Perrot on Lake St. Louis, in the St. Lawrence River (Quebec), showing the vegetation belts between the open water and the upland forest.

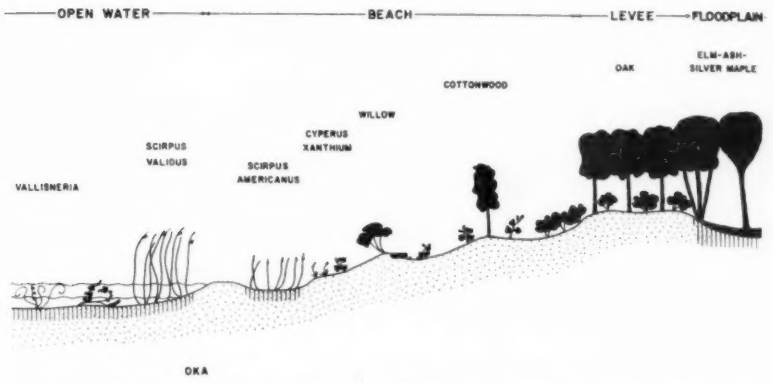


FIG. 9. The shoreline at Oka on the Lake of the Two Mountains, Lower Ottawa River (Quebec), showing the vegetation belts between the open water and the floodplain forest.

In the Champlain – St. Lawrence region, *Xanthium* does not usually germinate until July, does not flower until mid-August, does not ripen its fruits until October. The rhythm of the river and lake floods consists in a late-May high which overwhelms the floodplain (primevally and in most places still elm – ash – silver maple forest, very dark in summer) and an October low with a prolonged (early July – late September) stabilization at the point marked "summer water level" in Fig. 8. This means that points below this ("open water" in Figs. 5–9) are essentially aquatic (briefly emerged) and harbor no true land plants. The floodplain, on the other hand, and very frequently the levee where it is present, have an arborescent vegetation and are generally inhospitable to heliophilous plants. Where the cottonwoods, elms, ashes, etc., have been felled, a dense growth of shrubs, herbs, and grasses takes over and they tend to form a sod where competition allows almost no annual to root. Thus, in such a transect, the beach offers a substratum which is warm and dry at the surface, with plenty of light, and a seasonal washing off of débris (Fig. 10). In many places it is quite evident that the pulses of the receding flood deposit abundant seed, for the whole of the beach is occupied by parallel strips of vegetation separated by bare areas (Fig. 12).

The four localities sampled are shown in Figs. 5–13, which illustrate fairly well the range of the *Xanthium* shore habitat in eastern North America. The physiographic features of each one will be considered, the botanical composition of *Xanthium* communities will be analyzed, and some consideration will also be given to shoreline changes. Thereby the essentials of ecological pressure can be defined. Community analysis of the beach sector at Burlington, Venise, and Oka was made by quadrats of appropriate shape, generally totalling 200 m^2, and a record was made of coverage (see Table 3–13 and Fig. 3–39 in Dansereau 1957 (16)) and of *local coverage* (see Table 3–14

in Dansereau 1957 (16)). Another analytic consideration is *dispersal type*, for which the categories proposed by Dansereau and Lems (17) are used. These are transcribed in the following key.

OUTLINE KEY OF THE MAJOR DISPERSAL TYPES IN PLANTS*

D. does not disarticulate from the parent plant before being deposited at the site of further development. (Parent plant may be dead or alive at that time.) AUXOCHORE 1

D. disarticulates from the parent plant before the dispersal phase.

D. very voluminous in relation to the actual reproductive part, consisting of a loose spherical framework. CYCLOCHORE 2

D. consisting for the main part of the reproductive organ.

D. with scarious or stiff appendages.

Appendages thin, light, often flexible.

Appendages scarious, wing-like or saccate. PTEROCHORE 3

Appendages long, hairlike, or plumose. POGONOCHORE 4

Appendages short, stiff, spiny, or glandular, adhering to rough surfaces.....DESMOCHORE 5

D. without appendages (except for arils).

D. with juicy or fleshy outer layers. SARCOCHORE 6

D. with hard outer layer.

D. small or light enough to be carried by breeze. SPOROCHORE 7

D. too heavy to be carried by breeze.

Parent plant without mechanism of expulsion.

D. light enough to be carried by wind. SCLEROCHORE 8

D. very heavy.....BAROCHORE 9

Parent plant with mechanism of expulsion. BALLOCHORE 10

*According to a classification proposed by Dansereau and Lems (17). D = diaspore.

The data compiled in Table III show considerable evidence of heterogeneity. It has therefore seemed useful to group the species according to the phytosociological complexes of which they are most frequently (and sometimes

TABLE III

A phytosociological chart of beach communities in three localities: seven belts in Burlington (Vermont), two in Venise (southern Quebec), and two in Oka (central Quebec)

Species	E.i.	D.t.	L.f.	Burlington								Venise		Oka	
				7	6	5A	5B	4	3	2	1	2	1	2	1
Xanthium	F	5	Th	1.2	(·)	+ +	+ +	+ +	+ +			+ +	· ·	+ 1	+ +
Polygonum pensylvanicum var. *rosaefolium*	F	8	Th	+ +	2.2	1.4	+ +	1.2	+ +	1.3	.°.				
Cyperus rivularis	F	8	G				+ 1	3.5	3.5	1.2					
Cyperus inflexus	F	8	G				+ +	+ 1	+ 1						+ +
Cyperus houghtonii	F	8	G											+ +	+ +
Cyperus dentatus	F	8	G											· ·	· ·
Eragrostis pectinacea	F	8	Th		· ·		+ +							· ·	
*Mollugo verticillata**	F	8	Th	· ·	· ·	· +								· ·	
Polanisia graveolens	F	8	Th	+ +			.°.								
Puccinellia sp.	F	8	Th											· ·	
Potentilla anserina	F	1–8	H	.°.			· ·								
Polygonum punctatum	FD	8	Th					+ +	+ +	.°.					
Cyperus esculentus	FB	8	G		2.4	+ +	1.2	+ +	+ +						
Cenchrus pauciflorus	FB	5	Th	+ +		· ·									
Prunus susquehannae	FB	6	Ch											+ 3	· ·
Mentha canadensis	FB	8	H	· ·		· ·									
Apocynum cannabinum	FB	4	G									+ +			
Salix sp.	FB	4	Pp									· ·		1.1	
Vitis sp.	FC	6	Ps											+ 2	
Apios americana	FC	10	G											· ·	
Oenothera sp.	FG	8	Th	· +										1.1	· ·
Bidens frondosa	EF	5	Th	+ +	+ +	2.4	+ +	+ +	+ +	+ +	.°.			· ·	+ +
Echinochloa crus-galli	G	8	H	· ·	+ +		+°+	· ·	· ·						
Ambrosia artemisiifolia	G	8	Th	+ +	+ +	· ·		· ·	· ·					· ·	
*Polygonum convolvulus**	G	8	Th	· ·											
Asclepias syriaca	G	4	G	· ·										1.1	+ +
*Taraxacum officinale**	G	4	H	· ·											
*Solanum tuberosum**	G	1	G	· ·											
*Digitaria sanguinalis**	G	8	Th		· ·										
*Chenopodium album**	G	8	Th				.°.	· ·	· ·						
Amaranthus sp. *	G	8	Th				· ·								
*Galinsoga ciliata**	G	5	Th				· ·								
*Polygonum aviculare**	G	8	Th				· ·								
Equisetum arvense	G	1–7	G											· ·	
*Brassica nigra**	G	8	Th					· ·	· ·						
*Plantago major**	G	8	H					· ·	· ·						
*Rumex obtusifolius**	G	3	H										°.+		
Potentilla monspeliensis	G	8	H					· ·							
Onoclea sensibilis	C	7	H									· ·			
Lycopus americanus	C	8	H	+ 1			· ·					· ·	+ +		
Salix nigra	C	4	Pm	· +											
Ulmus americana	C	3	Pg											· ·	
Acer saccharinum	C	3	Pg										.°.		
Cornus stolonifera	CD	6	Pp	.°.										.°.	
Eupatorium purpureum	D	4	H	.°.											

TABLE III (*Concluded*)

A phytosociological chart of beach communities in three localities: seven belts in Burlington (Vermont), two in Venise (southern Quebec), and two in Oka (central Quebec)

Species	E.i.	D.t.	L.f.	Burlington								Venise		Oka	
				7	6	5A	5B	4	3	2	1	2	1	2	1
Calamagrostis canadensis	D	8	H	. .											
Spartina pectinata	D	8	G									3.4		. +	+ +
Penthorum sedoides	D	8	Ch									+ +	+ +		
Sium suave	D	5	H									+ +			
Hypericum boreale	D	8	Ch										+ +		
Hypericum sp.	D	8	H									. .			
Lysimachia terrestris	D	1	G									. .	+ 1		
Scirpus atrocinctus	D	8	G									.°.			
Gentiana sp.	D	8	H									. .			
Muhlenbergia mexicana	D	8	H											. .	
Juncus sp.	E	8	H											. .	. .
Eleocharis calva	E	1–8	G										1.3		
Scirpus americanus	E	1–8	G										1.2	. +	1.1
Sagittaria sp.	E	8	G									+ +	+ +		
Bidens cernua	DE	5	Th										. .		
Acer rubrum	BC	3	Pg		.°.									. .	. .
Salix humilis	BD	4	Pp												. .
Equisetum hyemale	BD	1–7	Ch											+ 1	
Pteridium aquilinum	B	7	G											. .	
Solidago rugosa	B	4	H											. .	
Aster lateriflorus	B	4	H										. .	+ 1	
Comptonia peregrina	B	5	Ch											1.3	
Andropogon gerardi	B	5	H											+ 1	
Panicum sp.	B	8	H			+ 1	. .			. .					
Populus deltoides	B	4	Pg											1.2	+ +
Rosa blanda	B	8	Ch											. .	
Solidago graminifolia	B	4	H											+ 1	
Apocynum androsaemifolium	BG	4	G											+ 1	

NOTE: The species are grouped in their order as "ecological indicators" (E.i.), from A to G (see text, page 195); the "dispersal type" (D.t.) is given as in the key (p. 192) and the Raunkiaer (38) "life form" (L.f.). The phytosociological figures are coverage and local coverage (as in Dansereau (16), Tables 3–13 and 3–14). The asterisk indicates naturalized species.

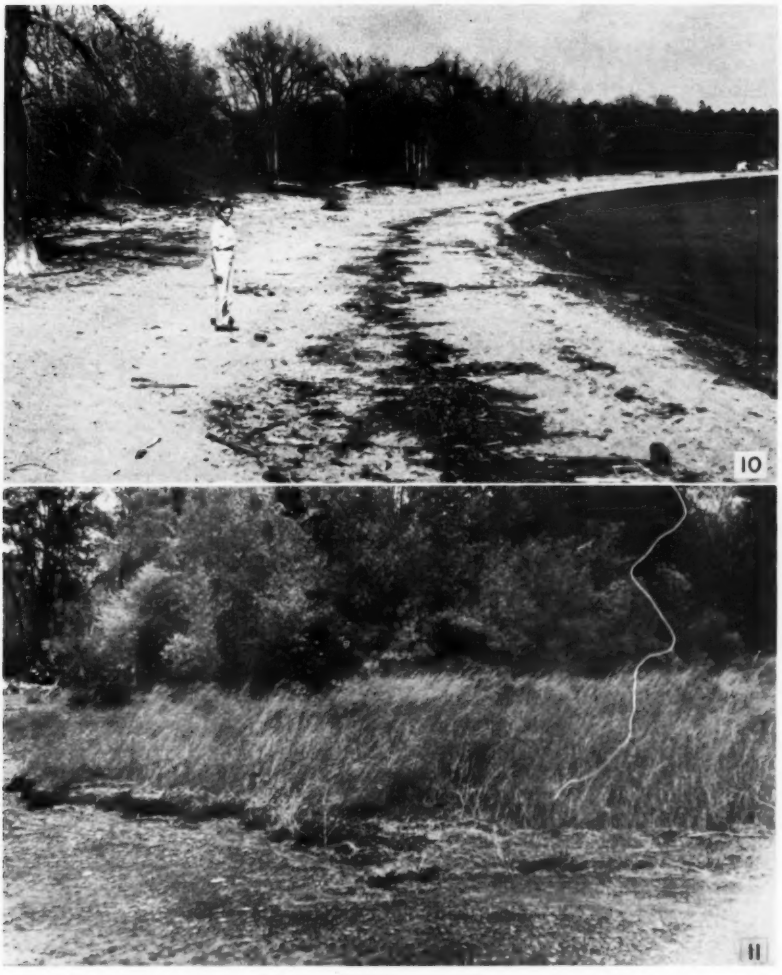


FIG. 10. The beach at Burlington (see Fig. 5), showing gentle slope and debris-accumulation line; at left, the floodplain forest.
FIG. 11. The beach at Venise (see Fig. 6) with dense growth of the *Scirpus* and *Spartina* belts in front of the low willow and high poplar stands.

FIG. 12. The shoreline at Ile Perrot (see Fig. 8), showing at least five successive but discontinuous belts of low herbaceous vegetation, corresponding to recession levels of the flood. At right, the floodplain forest.

FIG. 13. The beach at Oka (see Fig. 9) with its rather chaotic sand, harboring many tufts of shrubs. At left, the levee with oaks and poplars.

exclusively) members. Focussing as we have upon the beach, it seems useful to recognize seven habitats as potentially contributing to beach colonization, inasmuch as they all have contacts with it. The species are therefore labelled from A to G as follows:

A. *Mesophytic forest* species, usually present in well-drained upland, deeply shaded in summer. This is the Laurentian maple–beech climax forest. None of these are very likely to take root on the beach itself, although some will be found in the shaded levee, such as *Smilacina racemosa* and *Smilax herbacea*.

B. *Subxerophytic woodland* species, of open pine, aspen, oak, poplar, or birch communities, generally on porous soil. Most of these do not readily withstand flooding of any duration: *Vaccinium myrtilloides, Comptonia peregrina, Comandra umbellata, Gaultheria procumbens.* However, the levee (typically dominated by *Populus deltoides* in this region) presents a special case: either it is only very briefly under water, or as is the case at Oka (Fig. 9), it forms an island at high-water time (and is occupied by oak, pine, aspen instead of poplar). Typical levee plants are *Rhus radicans, Smilacina stellata, Vitis riparia, Apios americana, Strophostyles helvola.* The latter two are never found elsewhere in this region. (They show high fidelity.)

C. *Floodplain* species: the elm – ash – silver maple association harbors a number of typical plants not at all or not often found elsewhere: *Symplocarpus foetidus, Rhamnus alnifolia, Caltha palustris,* although they are able to persist after the destruction of the forest; and others that extend to many wet and shaded sites: *Impatiens capensis, Onoclea sensibilis.*

D. *Wet prairie* species belong to a great graminoid complex that grows densely on shores and marshes dominated by one or more of the following: *Calamagrostis canadensis, Spartina pectinata, Carex crinita,* etc. This category begs for further division, of course (see Dansereau 1956 (15) Fig. 16), into associations sensu stricto. But this is hardly necessary for our present purpose. Suffice it to recognize these conditions as a marsh (helophytic) site, in contrast to the following.

E. *Shallow aquatic* species (limnophytic complex). This includes the bulrushes (*Scirpus americanus, Sc. validus*), the spike rushes (*Eleocharis palustris, E. calva*), many of the rushes (*Juncus*), the arrowheads (*Sagittaria* spp.), etc.

F. *Beach* species. There are not too many plants in this area that show anything like complete fidelity to the beach. Many are also dune or sandplain species: *Asclepias syriaca, Ambrosia artemisiifolia.* Maybe *Cyperus rivularis, Potentilla anserina,* and *Xanthium* itself are the best examples.

G. Weeds such as *Taraxacum officinale, Brassica nigra.*

The list in Table III is revealing of both similarities and differences between the three localities, and some of these have been compiled in Table IV. Concerning the mentioned ecological indicators, the noteworthy features are the following:

1. There are no mesophytic species at all (A), although many, such as *Smilax herbacea, Smilacina racemosa,* are found on the levee, and others, such as *Dryopteris spinulosa, Maianthemum canadense,* in the floodplain.
2. Weeds (G) run very high at Burlington (especially in the organic débris as shown in Fig. 10) and very low in the close swards at Venise.
3. The beach plants proper (F) are most important in Burlington and it can be argued that Burlington presents the most typical beach conditions: quite sandy, compact and flat, open (Fig. 10); whereas Venise is silty, gravelly, and densely vegetated (Fig. 11); Oka, on the other hand, has the microrelief of a dune (Fig. 13).
4. This latter feature accounts for the high incidence of subxerophytes (B) at Oka.
5. Conversely the marsh plants (D) and shallow-water plants (E) are very much more abundant at Venise where the water-holding capacity of the soil and the check on evaporation are highest.
6. Floodplain species (C) also reach their highest percentage at Venise, although not an impressive one.

Turning now to life forms, the large representation of annuals is striking: almost half of the species at Burlington, but only a quarter at Oka and one tenth at Venise. In the latter the solid sod is composed of hemicryptophytes and geophytes that leave little room for the shifting therophytes. At Oka, the microdune conditions are most favorable to geophytes and to chamaephytes (absent in Burlington).

TABLE IV

A numerical comparison between the beach populations of the three localities recorded in Table III

Locality		Ecological class							Dispersal type										Life form				
		A	B	C	D	E	F	G	1	2	3	4	5	6	7	8	9	10	P	Ch	H	G	Th
Burlington	Total number, 35	0	3	3	3	0.5	11	14.5	1.5	0	1	4	4	1	0	23.5	0	0	3	0	10	5	17
	% of total	0	8.6	8.6	8.6	1.4	31.4	41.4	4.3	0	2.9	11.4	11.4	2.9	0	67.1	0	0	8.6	0	28.5	14.3	48.6
Venise	Total number, 20	0	2	3	8.5	3.5	2	1	2	0	2	3	3	1	0	9	0	0	2	2	7	7	2
	% of total	0	10.0	15.0	42.5	17.5	10.0	5.0	10.0	0	10.0	15.0	15.0	5.0	0	45.5	0	0	10.0	10.0	35.0	35.0	10.0
Oka	Total number, 33	0	11	3	3.5	2.5	9	4	1.5	0	2	8	4	3	2	11.5	0	1	7	4	6	9	7
	% of total	0	33.3	9.1	10.6	7.6	27.3	12.1	4.5	0	6.1	24.3	12.1	9.1	6.1	34.8	0	3.0	21.2	12.1	18.2	27.3	21.2

As for dispersal types and their distribution, the overwhelming majority belong to the nondescript sclerochores, 8 (see key), as is also the case in many aquatic communities. It is easy to understand how these small, light diaspores will remain on the beach, carried by occasional waves and also by wind. The effect of the latter is, however, most evident at Oka where the pogonochores, 4, are most numerous. As for the hooked type, 5, to which *Xanthium* belongs, it may not be represented by many species, but some of them are very distinctly beach plants (*Cenchrus*) or at least shore plants (*Bidens*, *Sium*).

In short, Burlington (Figs. 5 and 10) conveys a picture of the open beach, in a sense the perfect beach, where the flat, hard, sandy surface is principally molded by the periodic flood, not reshaped to any extent (as at Oka) by the summer winds. The pulsation of the receding waters is the principal agent that deposits, together with débris of all kinds (mostly organic), the seeds of plants that can be carried and that will germinate in the open light. Ile Perrot (Figs. 8 and 12) shows the same pattern somewhat foreshortened, with four instead of seven belts; the upper and lower contacts are, however, somewhat similar. At Venise, the humid silty substratum allows the bulrushes (confined to small depressions in the Oka beach) to reach higher in the gradient and practically to close the gap between the wet meadow and the levee.

Xanthium populations are almost nowhere of very high coverage. Indeed Table III shows that at both Venise and Oka they amount to hardly more than scattered individuals: wind and drought, lack of organic matter in the latter place, competition with graminoids in the former are not favorable and the plants are being *cornered* very badly. In order to meet with really dense populations, of *tall* vigorous plants bearing large quantities of fruits, one must turn to the ruderal habitats.

For instance, in Venise, the rock jetty shown in Fig. 7 is made of very coarse materials: boulders loosely assembled where sand and silt have variously infiltrated. Among the beach plants only a few have become established there besides *Xanthium*: *Polygonum persicaria*, *Bidens*, *Lysimachia terrestris*, *Polanisia graveolens*, *Mentha canadensis*. Although the biotope is very small (usually 3–8 in. in diameter), or maybe because of this, *Xanthium* competes well with these plants and even with the probably more aggressive weeds, such as *Chenopodium album*, *Linaria vulgaris*, *Polygonum convolvulus*, *Plantago major*.

In the same locality *Xanthium* is found in a grassy ditch, where the individual clumps are much taller, but more or less isolated.

Other ruderal situations are very numerous and even a cursory examination of many of them reveals that in these anthropogenic habitats *Xanthium* is again cornered. For instance, in vacant lots in the city of Montreal, *Xanthium* colonies grow 2 ft and more, have very broad leaves, fruit abundantly, and exclude all other species on freshly exposed sandy ground. At this stage it competes well with *Chenopodium album*, *Ambrosia artemisiifolia*, and possibly with *Echinochloa crus-galli* and *Vicia cracca*. But the encroachment of more vigorous biennials such as *Arctium* press it out and presently

the vigorous propagation of *Agropyron repens*, *Poa compressa*, and the staunch rosettes of *Artemisia vulgaris* and *Solidago altissima* crowd it out definitively.

In conclusion it can be stated that limiting factors in *Xanthium* ecology are as follows:

1. Preference for compact sandy soil, slightly moist below the surface and containing a small quantity of organic material. A beach not subject to pronounced eolian action is probably its optimum.
2. It can sometimes compete with other more delicate and smaller annuals but does not persist after consolidation of the sod, especially by graminoids.
3. It does not venture under the shade of even very open levee woodland.
4. Dispersal of the fruits is effected mostly by water.
5. Favorable ecological conditions for *Xanthium* cannot be found over large areas: only in somewhat protected coves with a long beach can the populations maintain themselves regularly over long periods of time; everywhere else a constant shifting is in order.

Physiological Responses

Xanthium has proved to be a most interesting material for physiological investigations, and to contain various chemicals, which are still being investigated. These seem to play rôles in the germination, growth, and flowering time of the plants, as well as being of certain medical importance. Some have also been used as drugs and dyes, and some seem to be very susceptible to changes in day length, which could of course be a strong limiting factor in their distribution pattern. (Regarding photoperiodism in *Xanthium*, see Nos. 50–83 in Part II of the References!)

In brief, studies of the photoperiod of *Xanthium* reveal that it is a decided short-day plant, which will not flower at all, or only with difficulty and very slowly develop floral parts, if the day length exceeds a maximum of 14 hours. Some variation in light-period requirement seems to exist among different strains (42). The 14 hours of day is exceeded from the end of June to the beginning of August, at Lat. 40°, and this seems to account for the late-summer flowering of this genus at northern latitudes. A certain amount of heat is also necessary for the seeds to germinate, and the regular life cycle of *Xanthium*, according to our own observations from Quebec, Manitoba, New England, the northern middle west states, as well as California, is late germination (end of June, early July), late summer flowering (August–September) irrespective of size reached by the plant, whether it has two leaves or hundreds of them, and seed ripening in the fall (September–October). The seeds fall off the plant during the winter, but may occasionally remain on the dry branches until the next spring or summer. The vegetative parts of the plant are strictly annual.

During the light hours of the day a hormone builds up in the leaves, which seems to prevent flowering, but a period of darkness destroys it again and thus induces flowering. When the critical light–dark balance is reached, the necessary dark period can be extremely short, and "dark" in this case also includes certain dark-red lights, to which the plants seem "blind". Darkness in the ordinary sense of the word is not necessary.

Though the physiologists seem practically unanimous about the short-day qualities of *Xanthium*, it is extremely difficult in most cases to get information as to the particular type of *Xanthium* which has been used in their experiments.

Most refer to their plants as "*X. pensylvanicum*," "*X. italicum*," "*X. canadense*," etc., but with the existing confusion of nomenclature, this does not clarify the situation. Very often the material seems to represent a local type of *Xanthium* from the vicinity of the place of experiment, if any indication at all is given as to the origin of it. There are of course cases where the experimenter has taken the trouble to let a taxonomist determine his material, a highly recommended practice that ought to be more general in physiological works. But, as matters stand, it is impossible for us to say, i.e., that "*X. chinense*" seems to react to a shorter day than *X.* "*oviforme*," and we can only draw one general conclusion: *Xanthium* is a short-day genus.

A very interesting feature is the variation in germination rate between the two seeds in the fruit. In a lot of cases, when the fruit is ripe, one seed is almost pushed out of its hollow (Fig. 14), and has therefore been named "upper seed" by physiologists. "Upper seeds" seem to germinate quicker (97), and in so doing prevent the "lower seed" from germinating. Many attempts have been made to explain this. The "lower seed" reputedly does not germinate till the next (or a later) season, after the "upper seed" has produced its plant. A continuation of the stand should thus be guaranteed. But there are also several cases reported of simultaneous germination of the two seeds, and it is not rare in nature to find "twin plants" which have obviously grown from the same fruit at the same time, and which often show a striking resemblance to each other in all characteristics: size, leaf, stalk, fruits, etc. Most likely different types of *Xanthium* differ with respect to seed germination. (Regarding seed germination in *Xanthium*, see Nos. 84–98 in Part III of the References!)

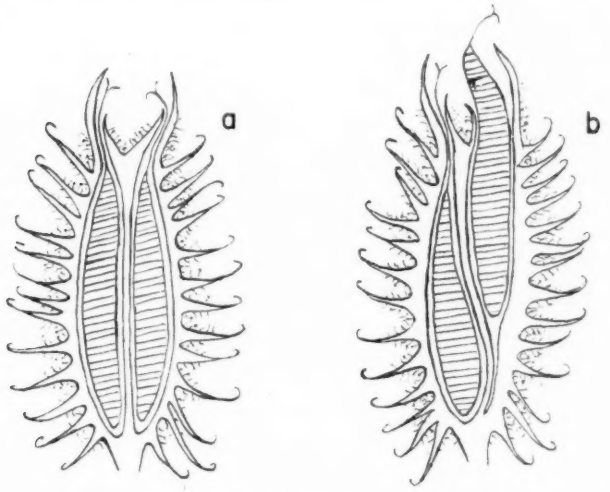


FIG. 14. *Xanthium* fruits showing position of: (*a*) normal seeds, and (*b*) "upper" and "lower" seeds in the bur.

Pollination Mechanism

There is so far no indication of apomixis in *Xanthium*. On the contrary, so many artificial crosses have been made successfully that obligate apomixis certainly does not prevail. Some lesser degree of facultative apomixis could occur, but is not necessary to explain the puzzling rates in character distribution which are revealed in natural populations. Experiments are, however, necessary in order to elucidate this point, and a study of fertility, morphology, and means of distribution of the pollen is also required before definite statements can be made. Such investigations are at present being carried out by Lascelles Nadeau at the Institut Botanique, Université de Montréal.

It has already been observed (Nadeau, unpublished) that the arrangement of the flowers in *Xanthium* favors inbreeding. The male flowers grow at the top of the main stalk or on the branches, above the female flowers. They start to shed pollen from the outermost stamens in the flower head a day or two before the stigmata are ready for pollination, and go on opening their anthers towards the center of the flower head until all female flowers are ripe. The slightest movement of the plant or a gust of wind makes the pollen rain down over the exposed stigmata of the female flowers immediately below. The pollen of the plant itself is therefore most likely to ensure the fertilization of its female flowers, and only an accident, a strong wind, crowded growth, or such, accomplishes cross-fertilization. Thus in *Xanthium* it seems that inbreeding is the rule and outbreeding only of occasional occurrence.

Biosystematical Aspects

No doubt crosses take place in nature between different types of *Xanthium*, and it is our opinion that such crosses have given rise, and are continuing to give rise, to an increasing number of "new species."

In America, we are thus inclined to surmise that originally one, at most two, forms of *Xanthium* (apart from *Acanthoxanthium*) existed, of which the primary one had a more or less glandular but also very hairy bur with medium coarse spines, densely set on the surface of the bur, and a rather prominent, straight to only slightly curved beak. This type was the same as, or very similar to, what we here have called the "*Cavanillesii*" complex and which has a predominantly tropical–subtropical distribution, reaching as far north as the southern parts of the United States, particularly in semidesert areas.

The other type, possibly developed out of the first one, should be a *Xanthium* with an often more than less glandular, but essentially hairless bur, the spines of which are somewhat shorter and more hooked. Its beak has a tendency to become more regularly curved and sometimes even hooked. This type roughly corresponds to what we have called the "*chinense*" complex.

Starting with the "*Cavanillesii*" complex in South and Central America we see a gradual evolution towards various types as the plants spread out over the North American continent. On the Pacific side there occurs a

gradual selection of plants with very big and very hairy fruits ending up in the extreme *oviforme* complex in the northwestern states (see map, Fig. 15). Through the central states over the prairies goes a stream of "hybrid" *pensylvanicum–italicum* types with all kinds of diversions in hairiness and size of fruit as well as length and shape of spines and beaks, and variations in day-length requirements. This line ends up in the northeastern states with the extreme *echinatum* complex (see map, Fig. 15). Along the Atlantic side of North America, we find in its southern part, particularly in the West Indies

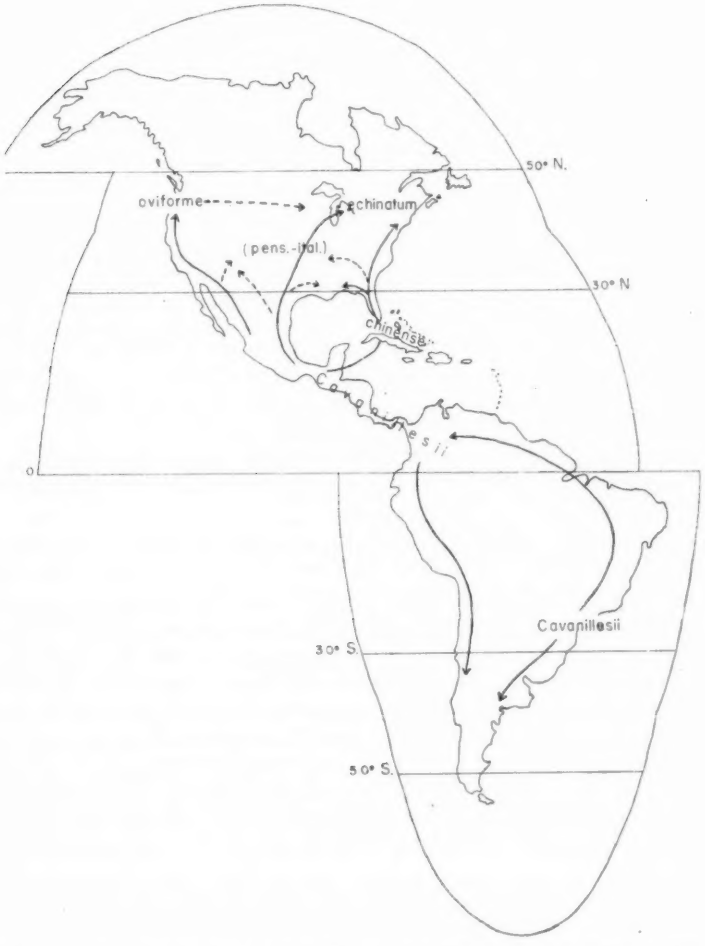


FIG. 15. Map showing hypothetical dispersal routes of *Xanthium* in South and North America.

and surrounding areas of the mainland, predominantly glabrate *chinense* types. These intergrade, especially on the mainland, with the *pensylvanicum–italicum* types, contributing to the hybrid nature of that complex (see map, Fig. 15).

Owing to the larger area covered by distinctly hairy types, one might also assume that these are older, and that the glabrous ones are more recent, but it may also be an expression of the recessive character of the genes for glabrous fruits. This is of course mere speculation till experiments have been carried out.

Our views of the development of the individual *Xanthium* types as outlined above are in contrast to Widder's ideas in the main part of his paper (46), but it must be noted that Widder in his Addendum expresses a tendency to reverse his standpoint. We feel that Widder's theory of a Beringia center, from which all American *Xanthium* should have dispersed from north towards south all the way to South America, is not tenable. It can claim no support from paleobotanical literature, and the short-day characteristic of the main body of types hardly calls for high latitudes as a center of dispersal. We therefore suggest that the development has followed the lines presented above and illustrated in the map (Fig. 15), and that the center of dispersal is tropical or subtropical, originating from a type of plant closely related to or the same as *X. Cavanillesii* Schouw.

We are, however, not ready at this stage in our investigations to propose a theory for the connections between the South American center of dispersal and that of the true *strumarium* forms in Europe, Africa, and Asia, but want to state that we are definitely of the opinion that they are pre-Columbian. Though we have not seen any material ourselves, we found evidence thereof in floras available to us. Cronquist (7, 8) states that *X. strumarium* occurs in tropical America.

It is also worth noticing that several genera related to *Xanthium*, for instance *Iva*, *Ambrosia*, *Franseria*, etc., seem to have "centers" in the dry areas of Central America – Mexico – northern South America.

The reason that this tropical–subtropical genus with a preference for dry habitats, but with a wide tolerance, has been able to disperse as far as the 50th parallel northwards, where probably day length puts it to a strong test, may possibly be sought in an extension of its potential area during the period of warmer, postglacial climate, often referred to as the "thermal maximum" or "hypsithermal period" (2, 5, 20, 49) in geological terms. Such an expansion—maybe even an "explosive" expansion—followed by a subsequent adjustment, ecologically and physiologically as well as genetically, to the new environment may account for a large part of the variation within this genus.

The original types are assumed to have grown and dispersed along rivers and shores, on sandbanks and dunes. As man entered the picture, however, he created new conditions, opened new habitats, and connected previously isolated ones, providing new means for the original forms to disperse and meet.

At present, a lot of opportunities, mostly man-made, avail for crosses between different populations, earlier isolated, and thus a multitude of new types emerge, which given time, may develop into stable units, depending on how they can stabilize and isolate themselves from additional new arrivals. In this connection, special attention should be given to the situation in New England, Quebec, and California, where European and/or Asiatic taxa may be variously involved in crosses with indigenous American stock.

In a stable and uniform population of *Xanthium* consisting of one type only, there is a small and limited variation of morphological characteristics. Where the population consists of more than one parental type, however, there is a wide range of variability of characters, as can be expected after hybridization, although there is a slight dominance of what we assume to be the original parental combinations of characters. In both kinds of populations the same degree of high pollen fertility prevails and seed setting is profuse. All *Xanthium* taxa so far known cytologically are tetraploids with $2n = 36$ chromosomes, and no barriers of sterility seem to have evolved within the subgenus. These facts, together with Nadeau's observations on the floral biology and the pollination mechanism, which will appear in a later work, lead us to assume that variation in a *Xanthium* population is the result of occasional hybridizations followed by a period of inbreeding and stabilization of the new character combinations in conformity with Mendelian expectations. This theory explains why many so-called "species" of *Xanthium* have very limited geographical areas, and are represented by a few herbarium sheets only, and it also explains why some of the "species" with a wide geographical range show such an amazing variability that delimitation becomes almost impossible. From a biosystematical point of view there is no doubt that the forms of *Xanthium* previously described as "species" are to be regarded as variations of a single species only. Taxonomists like Wiegand (48) and Cronquist (7, 8) have already reached this conclusion on morphological grounds alone.

The large species is, however, clearly divided into two major groups, geographically separate and morphologically distinct, though not intersterile: the American and the Mediterranean–Eurasiatic ones. It is appropriate from a biosystematical viewpoint to name them subspecies (Table V), as they are morphologically and physiologically regional groups of the same basic taxon, potentially and actually able to interbreed (32, 45).

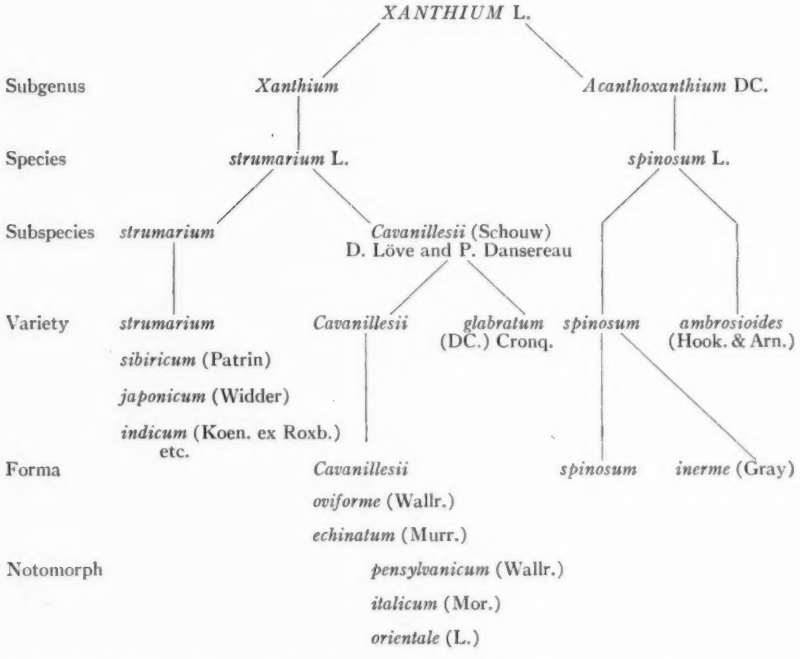
Prevalent inbreeding within each subspecies leads, however, to strong differentiation and to the emergence of distinct local populations. In America only one set of characters is of such general occurrence and of such geographical discreteness as to warrant a separation of two varieties: one widely distributed hairy variety, and one more limited glabrous one (6). In Eurasia, the size of the fruits seems to enable us to distinguish some varieties (Table V).

Within the population a system of general inbreeding combined with an occasional hybridization may, however, lead to a strong differentiation of local morphological types even to the point of isolation of "pure lines" in the

population as effectively as if these lines were isolated in space (42). In a diploid this could lead to a fast speciation even within small niches of a habitat, and may be the explanation of the situation in a large and critical genus as e.g. *Astragalus*. At the tetraploid level, as in *Xanthium*, the differentiation is assumed to be slower, and will not normally induce sterility barriers for a considerable period of time.

TABLE V

Classification of *Xanthium*
(in part provisional)



It is obvious that the classification into subspecies and varieties is insufficient for inclusion of the many taxa hitherto described in *Xanthium*. It is doubtful if a classification of all the segregates is possible or even desirable, since we now have a clue to their recent and hybrid origin. A few may have reached such a degree of stability and become so widely dispersed that they can be regarded as forms, but others are certainly only ephemeral types or recurrent hybrids, at best notomorphs. In Table V we have therefore preferred to treat this group in a provisional manner until we have accumulated enough experimental data for a more firm classification of these various minor entities. We feel confident, however, that we are now justified in transferring the following entity to the status of a subspecies: *Xanthium*

strumarium L. ssp. *Cavanillesii* (Schouw) D. Löve & P. Dansereau based upon *X. Cavanillesii* Schouw in Index seminum horti Academici Hauniensis anni 1849, Ann. Sci. Nat. 3. ser. (Bot. XII), p. 357.

The difficulty in classifying an apparently complex taxon like *Xanthium* seems to be caused mainly by the fact that such a polyploid species differentiates slowly into taxa separated by sterility barriers, and that hybridization can occur whenever already morphologically distinguishable and widely separated races meet, for instance through human interference. The most important fact is that after hybridization the new gene combinations soon become stable due to the high degree of inbreeding. This kind of evolution is certainly not very rare, and may often have defied the efforts of taxonomists, especially since it recalls the conditions known to occur in apomictic genera which occasionally hybridize. *Xanthium* is therefore a good example of a taxon with gradual speciation in a polyploid inbreeder with only occasional outbreeding, leading readily to morphological differentiation, while the formation of sterility barriers is correspondingly very slow.

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STUDIES ON SOLIDAGO L.

IV. THE CHROMOSOME NUMBERS OF CERTAIN TAXA OF THE GENUS SOLIDAGO[1]

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Abstract

The authors report the chromosome numbers of 25 taxa of the genus *Solidago* which had not yet been studied from this standpoint, and review the literature. The chromosome numbers of 42 taxa have now been published. The basic number of the genus is nine. Thirty-three taxa are diploid ($2n = 18$), five are tetraploid ($2n = 36$), three are aggregate taxa containing both diploid and tetraploid cytodemes, and one is hexaploid ($2n = 54$). Polyploidy has thus contributed to the evolution of the genus *Solidago* but it seems that most of the species have differentiated gradually. *S. decemflora* DC. of western North America differs from *S. nemoralis* Ait. of the same continent by morphological characters, its geographical distribution, and its chromosome number, the first taxon being tetraploid and the second diploid; the two are thus good species and not only varieties of the same species. The *S. rigida* of authors is an aggregate made up of two entities which are distinguished not only by their morphology and geographical distribution but also by their chromosome numbers; the eastern one (*S. rigida* L.) is tetraploid, whereas the western one (*S. parvirigida* Beaudry) is diploid. The bog and marsh goldenrods, *S. Purshii* and *S. uliginosa*, also possess different chromosome numbers, the first being diploid and the second tetraploid.

Introduction

Solidago L. is a genus of the tribe Astereae of the Compositae. It includes more than a hundred species, most of which are native to North America but with a few found in South America and in Eurasia.

It rates, with the genus *Aster*, among the taxonomically most difficult genera of the Compositae (18). Many of its entities are highly variable and the interspecific barriers of a large number of them are weak (18, 20, 22, 23).

The methods of classical taxonomy, as used by competent taxonomists like Fernald (18), Mackenzie (28), Friesner (19), and Cronquist (13), have revealed the existence of numerous complexities in this genus but it also becomes more and more evident that they cannot lead us to the solution of many of these problems. We can hope, however, that the methods of experimental taxonomy, added to those of classical taxonomy, will take us a few steps forward in the understanding of the origin of these complexities and of the limits between the entities of this genus.

The determination of chromosome numbers of all accessible taxa is one of the first items on the program when tackling a problem with the methods of experimental taxonomy. Knowledge of these numbers will provide the solution of certain taxonomic questions and information on the role of gradual speciation and polyploidy in the evolution of the group studied, on the origin and relationship of certain taxa, and on their crossing compatibilities.

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TABLE I

Chromosome numbers of taxa of the genus *Solidago* which have been determined by previous workers

Taxa	Chromosome numbers		Origin of the material	Workers
	Gametic	Somatic		
S. altissima L.	27	54	Quebec, Canada	Beaudry and Chabot (2)
S. × *asperula* Desf.	9	—	Nova Scotia, Canada and Massachusetts, U.S.A.	Goodwin (23)
S. canadensis L.	9	18	Quebec, Canada	Beaudry and Chabot (2)
	—	18*	?	Brock, *in* Darlington and Wylie (6)
	9	—	?	Carano (8)
S. chilensis Meyen	—	18	Cuyo, Agrentina	Covas and Schnack (11)
S. japonica Kitamura	—	18	?	Huziwara (25)
S. lepida var. *elongata* (Nutt.) Fern. (*S. elongata* Nutt.)	—	18	California, U.S.A.	Clausen, Keck, and Hiesey (10)
S. multiradiata Ait.	—	18	California, U.S.A.	Clausen, Keck, and Hiesey (10)
S. nemoralis Ait.	27	—	?	Morinaga and Fukushima (31)
S. Riddellii Frank	18		?	Carano (8)
S. parvirigida Beaudry (reported as *S. rigida* L.)	9	18	Indiana, U.S.A.	Higinbotham (24)
S. rugosa Mill.	9	—	Massachusetts, U.S.A., Nova Scotia and New Brunswick, Can.	Goodwin (23)
S. rugosa var. *aspera* (Ait.) Fern.	9	—	Massachusetts and Tennessee, U.S.A.	Goodwin (23)
S. sempervirens L.	9	—	Nova Scotia, Canada, and Massachusetts, U.S.A.	Goodwin (23)
S. sempervirens var. *mexicana* (L.) Fern.	9, 18	—	Maryland and Florida, U.S.A.	Goodwin (23)
S. Virgaurea L.	—	18	Budapest, Hungary	Baksay (1)
	—	18	Lapland, Sweden	Löve and Löve (27)
	9*	—	Austria	Mattick, *in* Tischler (30)
	9	18	?	Scheerer (35)
	—	18	Caucasus, U.S.S.R.	Sokolovskaia and Strelkova (37)
		18	Sweden, Norway, Finland	Turesson (38)
var. *alpestris* (Waldst. and Kit.) DC.	9	—	Switzerland	Rohner (33)
	—	18	Lapland, Sweden	Löve, *in* Selander (26)
var. *pumila* (Willd.) Gaudin	9	—	Switzerland	Rohner (33)
var. *vulgaris* (Lam.) Koch.	9	—	Switzerland	Rohner (33)

*Reported as such, but it is not possible to determine from this publication whether the actual count was made in gametic or in somatic cells.

Knowledge afforded by chromosome numbers, however, while always desirable, can be variously informative. Differences in the structure and morphology of the chromosomes can greatly enhance the insight dependent on mere numerical variations.

The authors have determined the chromosome numbers of different taxa of the genus *Solidago*, with the preceding ideas in mind, in an attempt to contribute to the advancement of our understanding of this most interesting genus. Little has yet been done, however, on the morphology of the chromosomes.

Review of the Literature

The chromosome numbers of 18 taxa of the genus *Solidago* have been determined by previous workers. Table I summarizes the pertinent data. It is clear that the basic number of the genus is nine. The number reported by Morinaga and Fukushima (31), for *S. nemoralis*, is subject to caution as will be explained later on.

Material and Methods

Most of our material comes from the province of Quebec, in which 36 localities have been sampled; the southern part of the province has been particularly well covered but some of our samples are from as far east as the localities of Marsoui, Murdochville, and Mt. Albert of the Gaspé Peninsula, as far north as the regions of La Tuque and Lake St. John, and as far northwest as the eastern and southern coasts of James Bay. In addition, other samples were obtained from Lockport, N.S.; James Bay, Ont.; Fort Saskatchewan, Alta.; New Canaan, Conn.; Dighton, Mass.; Mendon, Mass.; Rindge, N.H.; Albany, N.Y.; New Providence, Penn.; Bloomfield Hills, Mich.; and La Plata, Argentina.

One or more individuals have been sampled by a collection of living plants, of fruits, or of flower buds at each one of these localities. Root tips were obtained from the living plants. The fruits were used to produce seedlings which supplied additional root tips. The root tips were fixed in Karpechenko's fixative, sectioned at 15 μ, and stained with methyl violet 2B. The flower buds were fixed in Carnoy's fluid and used to determine gametic numbers in smears of microsporocytes stained with acetocarmine.

Our experience indicates that the freshly harvested mature fruits have to undergo a resting period of approximately two to three months (which cannot be broken or shortened by cold treatments) before reaching a germinable state; but this has not been clearly established by controlled experiments. In certain cases, root tips were pretreated in a saturated solution of paradichlorobenzene at 12–16° C for 3 hours before fixation.

Idiograms were drawn with a camera lucida at an initial magnification of ca. 5400×.

The plants which supplied the samples were pressed and dried and are kept in the herbarium of the senior author at the Institut Botanique of the Université de Montréal.

Analysis of the Data

Table II presents the collection numbers, names of collectors, localities of sampling, and chromosome numbers of the 164 samples of the taxa studied. A few numbers are preceded by the abbreviation ca. (circa) which means that these numbers could not be determined exactly. The numbers which follow the + sign refer to supernumerary chromosomes. The number of these chromosomes varies not only among individuals of the same taxon but also within the same individual; numbers occurring infrequently, as compared with others, are enclosed within parentheses. The collection numbers are composed of two or three sets of digits which are united by means of hyphens. The two-set numbers, like 55-140 or 55-144, refer to individual plants which were collected in nature. The three-set numbers, like 57-2-1 or 57-2-2, designate plants which were obtained in our cultures from plants collected in nature; three-set numbers in which the first two sets are identical designate sister plants. The abbreviations under "Collectors" refer to the following individuals: AC: A. Champagne; AD: A. Dutilly; DD: D. Doyon; DL: D. LaFontaine; EG: E. Galiano; EL: E. Lepage; ETW: E. T. Wherry; FCS: F. C. Seymour; FMS: Frère Marcellin-Sylvio; FRG: Frère Rolland-Germain; GHT: G. H. Turner; GRC: G. R. Cooley; HLC: H. L. Cabrera; JK: J. Kucyniak; JRB: J. R. Beaudry; LCM: L. Cinq-Mars; LM: Père Louis-Marie; MD: M. Duman; MR: M. Raymond; PD: P. Dansereau; RC: R. Cayouette; RG: R. Gauthier; WDL: W. D. Lambert; WPS: W. P. Stoutamire.

S. altissima L. is most commonly found in open places, dry or moist. Its northern limit extends from southern Quebec to Minnesota and its southern one from Florida to Arizona. Our counts show that it is a hexaploid species with a gametic number of 27 (Fig. 1) and a somatic one of 54 (Fig. 2).

S. arguta Ait. occurs mostly in open woods and clearings from southwestern Maine to southern Ontario in the north and from North Carolina, northern Alabama to Illinois in the south. Eighteen chromosomes have been found in its root tips (Fig. 3). This species has never been reported from the province of Quebec but a search in the territory adjacent to the states of New York and Vermont might lead to its discovery since it has been found in the vicinity of Plattsburg, N.Y., at approximately 25 miles from the Canadian–American border (information kindly supplied by Dr. E. C. Ogden, State Botanist, Albany, N.Y.).

S. bicolor L. var. *bicolor* is a plant of dry, open woods from Nova Scotia, the Magdalen Islands, southern Quebec to Wisconsin, and from Georgia to Arkansas. In Quebec, it is much less frequent in its habitat than further south. Its somatic number is 18 (Fig. 4).

S. caesia L. is found typically in rich woodlands. Its northern limit extends from Nova Scotia to Wisconsin and its southern one from Florida to Texas. Its $2n$ number is 18 (Fig. 5).

S. canadensis L. var. *canadensis* is a common entity in open moist or dry places from Newfoundland to Manitoba and from Virginia to Illinois. The high variability of its phenotype is the source of many taxonomic difficulties.

TABLE II

Chromosome numbers of different taxa of the genus *Solidago* L.

Taxa	Collection numbers	Collectors	Localities	Chromosome numbers	
				Gametic (n)	Somatic ($2n$)
S. altissima	55-140	JRB	L'Assomption (L'Assomption), Que.	27	
	55-144	JRB	L'Assomption (L'Assomption), Que.	27	
	55-179	DL	Montreal, Que.		ca. 54
	55-182	JRB	Richelieu (Rouville), Que.		54
	55-188	JRB	Longueuil (Chambly), Que.		ca. 54
	55-210	FMS	Lac Monroe (Montcalm), Que.		ca. 54 + 1 or 2
	55-210	JRB	St-Eustache (Deux-Montagnes), Que.		ca. 54 + 0 to 2
S. arguta	57-2-1	WDL*	New Canaan, Conn., U.S.A.*		18
	57-2-2	WDL*	New Canaan, Conn., U.S.A.*		18
	57-2-3	WDL*	New Canaan, Conn., U.S.A.*		18
S. bicolor var. *bicolor*	55-228	JRB & LM	Oka (Deux-Montagnes), Que.		18
S. caesia	55-173	DL	Montreal, Que.		18
	55-235	JRB	Montreal, Que.		18
	55-245	JRB & LM	Oka		18
S. canadensis var. *canadensis*	55-40	JRB, FRG, RG, & AC	St-Adolphe d'Howard (Argenteuil). Que.	9 + 0 or 1	
	55-120	DL	Rock Forest (Sherbrooke), Que,		18
	55-135	DL	Rock Forest (Sherbrooke), Que.		18
	55-175	DL	Montreal, Que.		18 + 2 or 3
	55-208	JRB	St-Eustache (Deux-Montagnes), Que.		18
	55-220	JRB	Lachute (Argenteuil), Que.		18 + 0 to 2
	56-494	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.		18
	56-495	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.		18 + 1
	57-19-1	FCS*	Mendon, Mass., U.S.A.*		18
	57-19-2	FCS*	Mendon, Mass., U.S.A.*		18
	57-19-3	FCS*	Mendon, Mass., U.S.A.*		18
S. canadensis var. *Hargeri*	55-225	JRB, DL, & EG	Longueuil (Chambly), Que.		18
S. chilensis	56-125-1	HLC*	La Plata, Argentina*		18
	56-125-2	HLC*	La Plata, Argentina*		18
	56-125-3	HLC*	La Plata, Argentina*		18
S. decemflora	55-279	GHT	Fort Saskatchewan, Alta.		36
S. flexicaulis	55-233	JRB	Montreal, Que.		18
	55-240	JRB	Oka (Deux-Montagnes), Que.		18

TABLE II (*Continued*)

Chromosome numbers of different taxa of the genus *Solidago* L.

Taxa	Collection numbers	Collectors	Localities	Chromosome numbers	
				Gametic (*n*)	Somatic (2*n*)
S. gigantea var. *gigantea*	56-278-1	JRB*	St-Hubert (Chambly), Que.*		36 + (1)
	56-278-2	JRB*	St-Hubert (Chambly), Que.*		36
	56-299-1	JRB & LCM*	Farnham (Missisquoi), Que.*		18
	56-299-2	JRB & LCM*	Farnham (Missisquoi), Que.*		18
	56-299-3	JRB & LCM*	Farnham (Missisquoi), Que.*		18
	56-303-1	JRB & LCM*	Farnham (Missisquoi), Que.*		18
	56-303-2	JRB & LCM*	Farnham (Missisquoi), Que.*		18
	57-21-1	FCS*	Mendon, Mass.*		18
	57-21-2	FCS*	Mendon, Mass.*		18
	57-21-3	FCS*	Mendon, Mass.*		18
S. gigantea var. *leiophylla*	55-83	JRB, DL, & FRG	Montreal, Que.	18	
	55-126	DL	Montreal, Que.		18 + 0 to 4
	55-212	JRB	Montreal, Que.		36
	55-226	JRB & LM	Oka (Deux-Montagnes), Que.		ca. 36
S. graminifolia var. *graminifolia*	57-6-1	AD, EL, & MD*	James Bay, Ont.*		18
S. graminifolia var. *Nuttallii*	55-113	JRB	L'Assomption (L'Assomption), Que.	9	
	55-153	DL	Capelton (Sherbrooke), Que.		18
	55-189	FMS	Lac Français (Terrebonne), Que.		18
	55-195	FMS	Lac Monroe (Montcalm), Que.		18
	55-199	JRB	St-André-Avellin (Papineau), Que.		18
	55-215	JRB	Ste-Geneviève-de-Pierrefonds (Jacques-Cartier), Que.		18
	55-218	JRB	Lachute (Argenteuil), Que.		18
	55-224	JRB & DL	Longueuil (Chambly), Que.		18
S. hispida var. *hispida*	55-168	JRB	La Tuque (Laviolette), Que.	9	
	55-190	FMS	La Conception (Labelle), Que.		18
	55-216	FRG & EG	Normandin (Lac St-Jean), Que.		18
S. juncea var. *juncea*	55-197	JRB	Longueuil (Chambly), Que.		18
	55-218	JRB, DL, & EG	Longueuil (Chambly), Que.		18
	56-369-1	RC*	St. Romuald (Lévis), Que.*		18
	56-369-2	RC*	St. Romuald (Lévis), Que.*		18
	56-369-3	RC*	St. Romuald (Lévis), Que.*		18
	57-25-1	FCS*	Mendon, Mass.*		18
	57-25-2	FCS*	Mendon, Mass.*		18

S. lepida var. *fallax*	55-271	LCM	Region of Lake St. John, Que.		18
	56-254	EL	Rimouski (Rimouski), Que.		18 + 1
	56-257	PD	Marsoui (Gaspé ouest), Que.		18
	56-264	PD	Murdochville (Gaspé ouest), Que.		18
	56-265	PD	Port Daniel (Bonaventure), Que.		18
	56-268	PD	Murdochville (Gaspé ouest), Que.		18
	56-269	PD	Murdochville (Gaspé ouest), Que.		18
S. macrophylla var. *macrophylla*	55-208	FMS	Lac Monroe (Montcalm), Que.		18 + 0 to 2
	56-258	PD	Marsoui (Gaspé ouest), Que.		18
	56-259	PD	Murdochville (Gaspé ouest), Que.		18
S. missouriensis	55-278-1	GHT*	Fort Saskatchewan, Alta.*		18
	55-278-2	GHT*	Fort Saskatchewan, Alta.*		18
S. multiradiata	56-529-1	DD*	Mont-Albert (Gaspé ouest), Que.*		18
	56-529-2	DD*	Mont-Albert (Gaspé ouest), Que.*		18
	56-529-3	DD*	Mont-Albert (Gaspé ouest), Que.*		18
S. nemoralis var. *nemoralis*	55-272-1	JK*	St. Jean (St. Jean), Que.*		18
	55-141	DL	Rock Forest (Sherbrooke), Que.		18
	55-221	JRB	Lachute (Argenteuil), Que.		18
	57-26-1	FCS*	Mendon, Mass.*		18 + 1
	57-26-2	FCS*	Mendon, Mass.*		18 + 2
	57-26-3	FCS*	Mendon, Mass.*		18 + 2 and 3
S. parvirigida	55-580-2	GHT*	Fort Saskatchewan, Alberta*		18
S. patula var. *patula*	57-147	JRB & GRC	Albany, N.Y.		18
S. puberula var. *puberula*	55-162	JRB	La Tuque (Laviolette), Que.	9	
	57-27-1	FCS*	Rindge, N.H.*		18
	57-27-2	FCS*	Rindge, N.H.*		18
	57-27-3	FCS*	Rindge, N.H.*		18
S. Purshii	55-152	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.	9	
	55-275	MR & LCM	Farnham (Missisquoi), Que.		18
	56-261	PD	Murdochville (Gaspé ouest), Que.		18
	56-262	PD	Murdochville (Gaspé ouest), Que.		18
	56-263	PD	Murdochville (Gaspé ouest), Que.	9	
	56-267	PD	Murdochville (Gaspé ouest), Que.		18 + 1
	56-280-1	JRB*	St-Hubert (Chambly), Que.*		18 + 1 or 2
	56-286-1	JRB*	Rougemont (Rouville), Que.*		18 + 2 (1)
	56-286-2	JRB*	Rougemont (Rouville), Que.*		18 + 2 (1 + 4)
	56-286-3	JRB*	Rougemont (Rouville), Que.*		18 + 2 (1)
	56-288-1	JRB*	Rougemont (Rouville), Que.*		18
	56-288-2	JRB*	Rougemont (Rouville), Que.*		18
	56-288-3	JRB*	Rougemont (Rouville), Que.*		18
	56-290-1	JRB & LCM*	Farnham (Missisquoi), Que.*		18
	56-290-2	JRB & LCM*	Farnham (Missisquoi), Que.*		18
	56-290-3	JRB & LCM*	Farnham (Missisquoi), Que.*		18

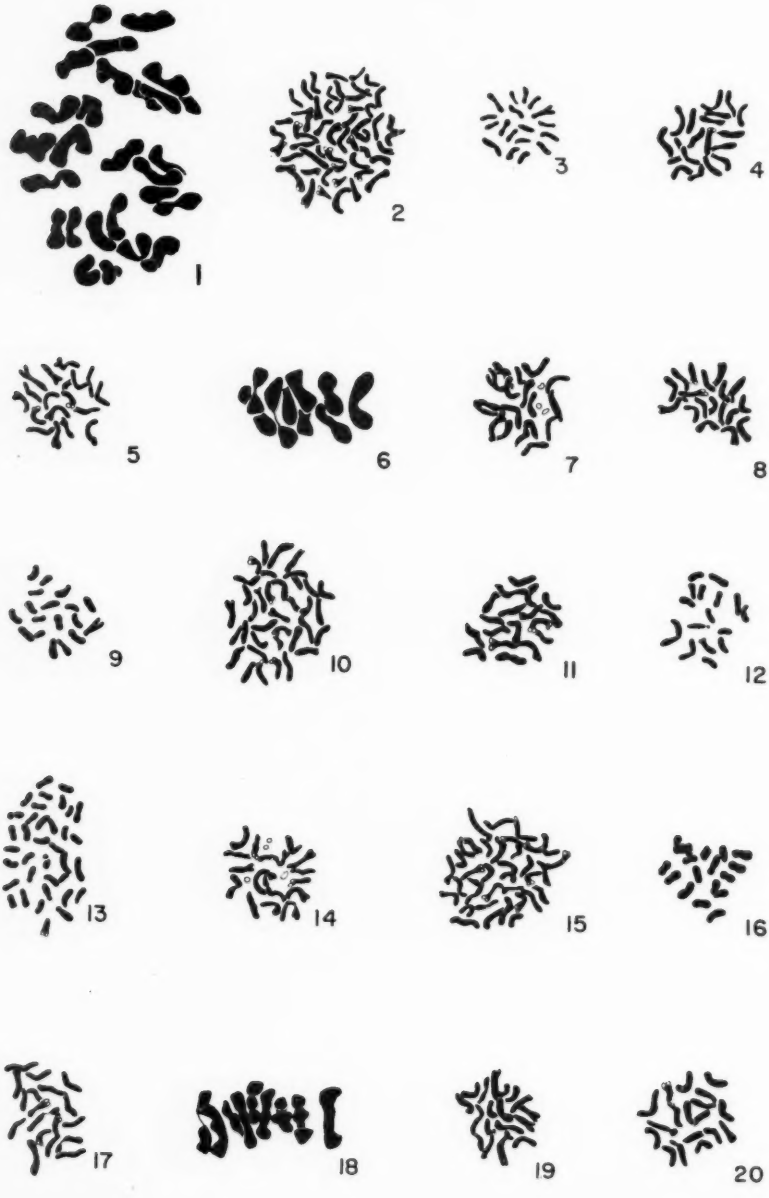
TABLE II (*Concluded*)

Chromosome numbers of different taxa of the genus *Solidago* L.

Taxa	Collection numbers	Collectors	Localities	Chromosome numbers	
				Gametic (n)	Somatic ($2n$)
S. Purshii	56-291-1	JRB & LCM*	Farnham (Missisquoi), Que.*		18
	56-291-2	JRB & LCM*	Farnham (Missisquoi), Que.*		18
	56-311-1	JRB & LCM*	Knowlton (Brome), Que.*		18 + 1
	56-311-2	JRB & LCM*	Knowlton (Brome), Que.*		18 + 0 or 1
	56-311-3	JRB & LCM*	Knowlton (Brome), Que.*		18 + 0 or 1
	56-312-1	JRB & LCM*	Knowlton (Brome), Que.*		18 + 1 or 2
	56-312-2	JRB & LCM*	Knowlton (Brome), Que.*		18
	56-312-3	JRB & LCM*	Knowlton (Brome), Que.*		18
	56-313-1	JRB & LCM*	Knowlton (Brome), Que.*		18
	56-324-1	JRB & LCM*	Coleraine (Mégantic), Que.*		18
	56-324-2	JRB & LCM*	Coleraine (Mégantic), Que.*		18
	56-413-1	JRB & LCM*	Lemieux (Nicolet), Que.*		18 + 2
	56-413-2	JRB & LCM*	Lemieux (Nicolet), Que.*		18 + 4
	56-413-3	JRB & LCM*	Lemieux (Nicolet), Que.*		18 + 2 and 4
	56-415-2	JRB & LCM*	Lemieux (Nicolet), Que.*		18
	56-415-3	JRB & LCM*	Lemieux (Nicolet), Que.*		18
	56-482	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.		18
	56-483	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.		18
	56-484	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.		18
	56-485	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.		18
	56-486	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.		18
	56-488	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.		18
	56-489	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.		18
	56-490	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.		18
	56-492	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.		18
	56-493	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.	9	
	57-7-1	AD & EL*	Oriental Watershed of James Bay, Que.*		18
S. Purshii × *S. rugosa*	56-488	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.		18
	56-491	JRB & FRG	St-Adolphe d'Howard (Argenteuil), Que.	9	18
S. Randii	56-433	JRB & LCM	Black Lake (Mégantic), Que.		36
S. rigida var. *rigida*	57-14-1	WPS*	Bloomfield Hills, Mich.*		ca. 36
	57-14-2	WPS*	Bloomfield Hills, Mich.*		36
S. rugosa var. *rugosa*	55-191	FMS	Lac Monroe (Montcalm), Que.		18
	55-200	JRB	St-André-Avellin (Papineau), Que.		18
	57-28-1	FCS*	Dighton, Mass.*		18

S. rugosa var. *rugosa*	57-28-2	FCS*	Dighton, Mass.*		18
	57-28-3	FCS*	Dighton, Mass.*		18
S. sempervirens	55-217	FRG & EG	Baie St-Paul (Charlevoix), Que.		18
	55-264	RG, AC, & EG	Lockport, N.S.	9	
	57-23-1	FCS*	Dighton, Mass.*		18 + 1
S. spathulata var. *neo-mexicana*	55-276-3	GHT*	Fort Saskatchewan, Alta.*		18
	55-276-4	GHT*	Fort Saskatchewan, Alta.*		18
	55-276-5	GHT*	Fort Saskatchewan, Alta.*		18
S. squarrosa	55-161	JRB	Charrette (St-Maurice), Que.	9	
	55-205	JRB	Pointe-au-Chêne (Argenteuil), Que.		18
S. tenuifolia	57-24-1	FCS*	Dighton, Mass.*		18
S. uliginosa	55-250	JRB & LM	Oka (Deux-Montagnes), Que.		36
	56-531	JRB & LM	Oka (Deux-Montagnes), Que.		36
	56-532	JRB & LM	Oka (Deux-Montagnes), Que.		36
	56-533	JRB & LM	Oka (Deux-Montagnes), Que.		36
	56-534	JRB & LM	Oka (Deux-Montagnes), Que.		36
	56-535	JRB & LM	Oka (Deux-Montagnes), Que.		36
	57-29-2	FCS*	Mendon, Mass.*		36
	57-29-3	FCS*	Mendon, Mass.*		36
	57-229	JRB & ETW	New Providence, Penn.		36
	57-230	JRB & ETW	New Providence, Penn.		36

*Collector(s) and locality of the mother plant, i.e., that which supplied the fruits from which the plants referred to here were grown.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Our samples establish that it is a diploid species with a gametic number of 9 (Fig. 6) and a somatic one of 18 (Fig. 7).

S. canadensis var. *Hargeri* Fern. has ecological requirements apparently similar to those of var. *canadensis*. According to Fernald (18), its range extends from southwestern Quebec to Michigan in the north, and from western New England, West Virginia, Tennessee, and Illinois in the south. Data kindly supplied by Doctors M. Fogg and E. T. Wherry for Pennsylvania show that it is more common in that state than var. *canadensis*. Its somatic number is identical with that of the typical variety (Fig. 8).

S. chilensis Meyen is a South American species which, according to Cabrera (7), is "very frequent in moist places." Its somatic number is 18 (Fig. 9).

S. decemflora DC. (*S. diffusa* A. Nelson, Bull. Torr. Botan. Club, 25, 378 (1898); *S. pulcherrima* A. Nelson, Bull. Torrey Botan. Club, 25, 549 (1898); *S. longipetiolata* Mack. & Bush, Trans. Acad. Sci. St. Louis, 12, 87 (1902); *S. nemoralis* var. *longipetiolata* (Mack. and Bush) Palmer and Steyerm., Ann. Mo. Botan. Gard. 22, 660 (1935); *S. nemoralis* var. *decemflora* (DC.) Fern., Rhodora, 38, 226 (1936)). This species occurs in dry soils from western Ontario to Alberta, and from Kentucky to Arizona. It is tetraploid with $2n = 36$ (Fig. 10).

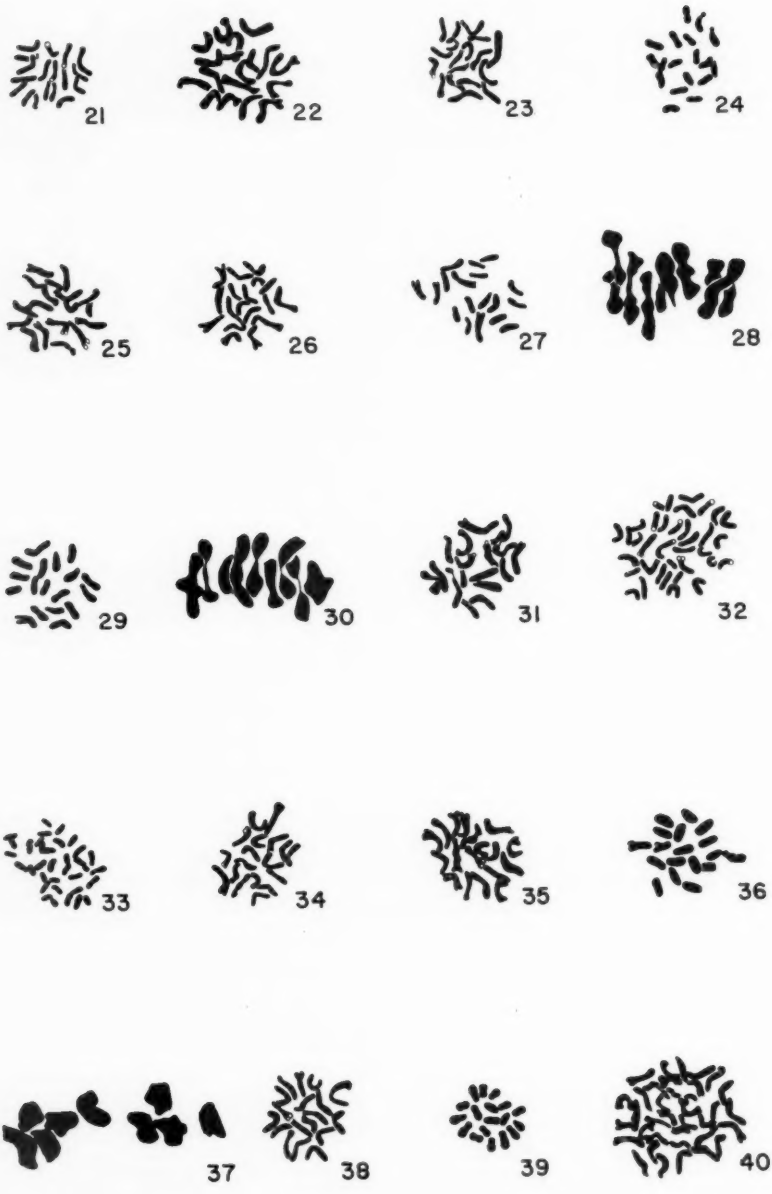
S. flexicaulis L. is commonly associated with *S. caesia* in rich woodlands from Nova Scotia and the Gaspé Peninsula to North Dakota and from Georgia to Arkansas. It is also a diploid entity with a $2n$ number of 18 (Fig. 11).

S. gigantea Ait. var. *gigantea* is a very widely distributed taxon occurring in moist, open places from Prince Edward Island to British Columbia and from Florida to New Mexico. It contains two cytodemes, a diploid one with a $2n$ number of 18 (Fig. 12) and a tetraploid one with a $2n$ number of 36 (Fig. 13).

S. gigantea var. *leiophylla* Fern. is found throughout the range of the preceding variety and in similar habitats. It also contains two cytodemes at the same levels of ploidy: $2n = 18$ (Fig. 14) and 36 (Fig. 15).

S. graminifolia (L.) Salisb. var. *graminifolia* occurs in moist or dry open places from northern Quebec to James Bay and from Nova Scotia, New England, West Virginia, Iowa to South Dakota. Its somatic number is 18 (Fig. 16).

FIGS. 1–20. All ×1800. (*p*) = pretreatment with paradichlorobenzene. Fig. 1. *S. altissima*, 55-140, $n = 27$. Fig. 2. *S. altissima*, 55-182, $2n = 54$. Fig. 3. *S. arguta*, 57-2-1, $2n = 18$ (*p*). Fig. 4. *S. bicolor* var. *bicolor*, 55-228, $2n = 18$. Fig. 5. *S. caesia*, 55-235, $2n = 18$. Fig. 6. *S. canadensis* var. *canadensis*, 55-40, $n = 9$. Fig. 7. *S. canadensis* var. *canadensis*, 55-175, $2n = 18+3$. Fig. 8. *S. canadensis* var. *Hargeri*, 55-225, $2n = 18$. Fig. 9. *S. chilensis*, 56-125-1, $2n = 18$ (*p*). Fig. 10. *S. decemflora*, 55-279, $2n = 36$. Fig. 11. *S. flexicaulis*, 55-240, $2n = 18$. Fig. 12. *S. gigantea* var. *gigantea*, 57-21-2, $2n = 18$ (*p*). Fig 13. *S. gigantea* var. *gigantea*, 56-278-2, $2n = 36$ (*p*). Fig. 14. *S. gigantea* var. *leiophylla*, 55-126, $2n = 18+4$. Fig. 15. *S. gigantea* var. *leiophylla*, 55-212, $2n = 36$. Fig. 16. *S. graminifolia* var. *graminifolia*, 57-6-1, $2n = 18$ (*p*). Fig. 17. *S. graminifolia* var. *Nuttallii*, 55-224, $2n = 18$. Fig. 18. *S. hispida* var. *hispida*, 55-168, $n = 9$. Fig. 19. *S. hispida* var. *hispida*, 55-216, $2n = 18$. Fig. 20. *S. juncea* var. *juncea*, 55-218, $2n = 18$.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S. graminifolia var. *Nuttallii* (Greene) Fern. also inhabits moist or dry open places from Newfoundland to Minnesota and "...reputedly to Fla. and Ala...." (13). Its somatic number is 18 (Fig. 17).

S. hispida Muhl. var. *hispida* is a variable entity most commonly found in dry woodlands or on rocky shores from Newfoundland to Manitoba and from Georgia to Arkansas. A number of 9 has been counted in its microsporocytes (Fig. 18) and one of 18 in its root tips (Fig. 19).

S. juncea Ait. var. *juncea* is a species of dry open soils from Nova Scotia to Saskatchewan and from Georgia to Missouri. It is diploid, with $2n = 18$ (Fig. 20).

S. lepida DC. var. *fallax* Fern. is found, according to Fernald (18), from Newfoundland to British Columbia, south to southern Quebec, Lake Huron, Ont., northern Michigan and Minnesota, and Colorado, and grows in "moist to dryish thickets, shores and banks." The material that we refer to this taxon is from the region of Lake St. John and the Gaspé Peninsula of Quebec. Its $2n$ number is 18 (Fig. 21).

S. macrophylla Pursh var. *macrophylla* inhabits cool and damp woodlands from Newfoundland and southern Labrador to Lake Superior, Ontario, and south to the mountains of New England and New York. It is a diploid species with $2n = 18$ (Fig. 22).

S. missouriensis Nutt. occurs in prairies and other dry places from Ontario, Manitoba to British Columbia and from Tennessee to Arizona. Its somatic number is 18 (Fig. 23).

S. multiradiata Ait. is a subarctic-alpine species ranging from Gaspé, Newfoundland, northern Labrador, Ungava to Alaska, north beyond the tree line and down the Rocky Mountains. It is also diploid with $2n = 18$ (Fig. 24).

S. nemoralis Ait. var. *nemoralis* is very common in dry and open soils from Prince Edward Island, southern Quebec to North Dakota and from Georgia to Texas. Its somatic number is 18 (Fig. 25).

S. parvirigida Beaudry (cf. infra) is found in dry open places from Manitoba, Minnesota, and Iowa westward. Its somatic number is 18 (Fig. 26).

S. patula Muhl. var. *patula* is an entity of swamps and other wet places ranging from Vermont, southern Ontario to Minnesota, and from Florida to Texas. Its somatic number is 18 (Fig. 27).

FIGS. 21–40. All ×1800. (*p*) = pretreatment with paradichlorobenzene. Fig. 21. *S. lepida* var. *fallax*, 56-264, $2n = 18$. Fig. 22. *S. macrophylla* var. *macrophylla*, 55-208, $2n = 18$. Fig. 23. *S. missouriensis*, 55-278, $2n = 18$. Fig. 24. *S. multiradiata*, 56-529-1, $2n = 18$ (*p*). Fig. 25. *S. nemoralis* var. *nemoralis*, 55-221, $2n = 18$. Fig. 26. *S. parvirigida*, 55-280, $2n = 18$. Fig. 27. *S. patula* var. *patula*, 57-147, $2n = 18$ (*p*). Fig. 28. *S. puberula* var. *puberula*, 55-162, $n = 9$. Fig. 29. *S. puberula* var. *puberula* 57-27-1, $2n = 18$. Fig. 30. *S. Purshii*, 55-152, $n = 9$. Fig. 31. *S. Purshii*, 55-262, $2n = 18$. Fig. 32. *S. Randii*, 56-433, $2n = 36$. Fig. 33. *S. rigida* var. *rigida*, 57-14-2, $2n = 36$ (*p*). Fig. 34. *S. rugosa* var. *rugosa*, 55-191, $2n = 18$. Fig. 35. *S. sempervirens*, 55-217, $2n = 18$. Fig. 36. *S. spathulata* var. *neomexicana*, 55-276-3, $2n = 18$ (*p*). Fig. 37. *S. squarrosa*, 55-161, $n = 9$. Fig. 38. *S. squarrosa*, 55-205, $2n = 18$. Fig. 39. *S. tenuifolia*, 57-24-1, $2n = 18$ (*p*). Fig. 40. *S. uliginosa*, 55-250, $2n = 36$.

S. puberula Nutt. var. *puberula* is scattered here and there in dry sterile grounds from Cape Breton, the Magdalen Islands to Lake St. John, Que., and from Florida to Mississippi. Its gametic number is 9 (Fig. 28) and its somatic one 18 (Fig. 29).

S. Purshii Porter is typically a plant of bogs, marshes, and other moist places from Newfoundland, Labrador, Ungava to Manitoba; in the south it has been found as far as West Virginia, according to Fernald (18). It is diploid: $n = 9$ (Fig. 30), $2n = 18$ (Fig. 31). The 36-chromosome plants reported by Beaudry *et al.* (3) should be referred to *S. uliginosa*.

S. Randii (Porter) Britt. is found locally on magnesian or granitic rocks in Nova Scotia, southeastern Maine, the Eastern Townships of the province of Quebec, and the mountains of northern New York. It is a tetraploid entity with a somatic number of 36 (Fig. 32).

S. rigida L. var. *rigida* is found in dry and open places from Massachusetts to Minnesota and from Georgia to Texas. Its somatic number is 36 (Fig. 33).

S. rugosa Mill. var. *rugosa* is an entity of open woods and of borders of woods and rivers from Newfoundland, Quebec, and Ontario in the north and from western Virginia, Georgia, and Louisiana in the south. Eighteen chromosomes have been found in its root tips (Fig. 34).

S. sempervirens L. grows in saline and other moist habitats along the coast from western Newfoundland, the Gulf of St. Lawrence, and, on the Atlantic seashore, to New Jersey and locally to Virginia. It is diploid with a somatic number of 18 (Fig. 35).

S. spathulata DC. var. *neomexicana* (Gray) Cronq. is from prairies, open woods, bluffs, and other dry habitats from the District of Mackenzie, Yukon, Alberta, Saskatchewan, and along the Rocky Mountains to New Mexico and Arizona. It is diploid with a somatic number of 18 (Fig. 36).

S. squarrosa Muhl. is scattered throughout its range in rocky woodlands and clearings from eastern Quebec to southern Ontario, and from New Brunswick, Delaware to southern Indiana, and in the uplands of Kentucky and North Carolina. Its gametic number is 9 (Fig. 37) and its somatic one 18 (Fig. 38).

S. tenuifolia Pursh is found in "open sandy places near the coast, N.S. and Mass. to Fla. and probably La." (13). Its somatic number is 18 (Fig. 39).

S. uliginosa Nutt. is a plant of bogs, marshes, and other moist habitats from Nova Scotia, southern Maine, southern Vermont, southern Quebec, southern Ontario, southern Michigan, and Wisconsin, and from Delaware to the uplands of North Carolina. It is a tetraploid entity with a somatic number of 36 (Fig. 40).

A natural hybrid between *S. Purshii* and *S. rugosa* has been found at St-Adolphe d'Howard, Que. It is diploid like its putative parents.

Beaudry and Chabot (2) have already discussed the relationship of *S. altissima*, a hexaploid entity, with the diploid *S. canadensis*, and pointed out that in addition to this cytological difference, morphological, phenological,

and distributional data justify the conclusion that these two taxa should be considered as distinct species and not just as subspecific entities of an aggregate specific unit. The difference in chromosome number between *S. altissima* and *S. canadensis* indicates, on theoretical grounds, that they should be well isolated by a sterility barrier in the part of their range where they are sympatric. Our experience in southern Quebec where the two species are very common and grow in large intermixed colonies strongly supports this deduction. Hybrids between these two species have been reported by Fernald (18) and Marie-Victorin (29). Inspection of Marie-Victorin's hybrid specimen has convinced us that it is only a variant of *S. altissima*.

The numbers reported here for *S. canadensis* confirm those of Beaudry and Chabot, of Brock, and of Carano (Table I).

The chromosome number that we report for *S. chilensis* also confirms that of Covas and Schnack (Table I).

The plant named *S. decemflora* by De Candolle has been considered as a variety of *S. nemoralis* Ait. by some authors and as specifically distinct by others (see p. 219). It differs from *S. nemoralis* not only by its morphology and geographical distribution but also by its chromosome number since it is tetraploid whereas *S. nemoralis* is diploid. It is thus worthy of specific recognition and should be designated by the binomial of De Candolle.

The existence of two cytodemes (21), one diploid and the other tetraploid, has been established for two taxa: *S. gigantea* var. *gigantea* and *S. gigantea* var. *leiophylla*. In the first of these taxa, the diploid and the tetraploid cytodemes have been collected in different localities: the diploid is known from two localities, Farnham, Que., and Mendon, Mass., and the tetraploid from only one, St. Hubert, Que. In *S. gigantea* var. *leiophylla* the diploid cytodeme is known from one locality (Montreal, Que.) and the tetraploid from two (Montreal and Oka, Que.). Convenient taxonomic characters that would permit segregation of the two units of each one of these taxa have not been found but little time has yet been spent in this attempt. It is evident that much more work has to be done before the nature of these aggregate taxa can be understood since the diploid and the tetraploid individuals of the *S. gigantea* complex are very much alike.

The individuals here referred to *S. lepida* var. *fallax* are all from lower Quebec. Fernald (15) was the first to point out that in this region, and in Newfoundland, southern Labrador, and northern New Brunswick and northern Maine, *S. canadensis* is largely replaced by a common goldenrod, very much like the latter species, but with larger heads. He related that plant to the *S. lepida* of De Candolle and divided it into four varieties. To anyone somewhat familiar with the plants ascribed to *S. lepida* throughout North America, it is evident that they constitute a poorly understood complex. The lower Quebec plants studied here are no doubt distinct from *S. canadensis*. We are presently attributing them to *S. lepida* var. *fallax*, but this status may have to be modified when *S. lepida* will be better understood.

The chromosome number of 18 that we have determined for *S. multiradiata* from individuals originating from the Gaspé Peninsula confirms the one reported by Clausen, Keck, and Hiesey for individuals collected in California (Table I).

According to Morinaga and Fukushima (Table I), *S. nemoralis* is hexaploid with a $2n$ number of 54. Our determinations, made on plants of three different localities of the province of Quebec and on one from northeastern United States, show that this species is diploid. The Japanese authors do not state the origin of their material. Moreover, it is doubtful that they were dealing with a *Solidago* since the chromosomes that they illustrate are much smaller than those of all the taxa of *Solidago* that we have studied until now.

Porter (32) effected the segregation of the eastern and western populations of *S. rigida* L., in 1874, when he designated the latter as *S. rigida humilis*. The western segregate was recognized by Rydberg in 1904 (34), who gave it specific status in the genus *Oligoneuron* (*O. canescens*). Rydberg (*loc. cit.*), Breitung (5), Cronquist (13), and Boivin (4) have listed the morphological characters which permit the separation of the two classes of individuals. We have found 18 chromosomes in individuals from Alberta, Higinbotham (24) counted the same number in specimens from Indiana, and we have determined 36 chromosomes in individuals from Bloomfield, Mich., which evidently belong to the eastern entity. Since the western and eastern populations are differentiated not only by their morphology and geography but also by their chromosome numbers, it seems preferable to consider them as constituting different species and designate the western individuals as *Solidago* **parvirigida** Beaudry nom. nov., based on *S. rigida humilis* Porter, Syn. Fl. Colo. 63, 1874; not *S. humilis* Mill. (as *S. humilius*), Gard. Dict. ed. VIII, no. 16, 1768; not *S. humilis* Pursh, Fl. Am. Sept. II, 543, 1814; not *S. humilis* Desf., Cat. Hort. Par. ed. III, 402, 1829. Synonyms: *Oligoneuron canescens* Rydb., Bull. Torrey Botan. Club, 31, 652 (1904); *S. canescens* (Rydb.) Friesner, Butler Univ. Botan. Studies, 4, 196 (1940) (not *S. canescens* Sessé & Moc. La Naturaleza, 2 ser., I, 1887–1890, app., p. 141); *S. rigida* var. *canescens* (Rydb.) Breitung, Can. Field Nat. 61, 100 (1947).

The bog and marsh goldenrods, which have been variously named *S. uliginosa* Nutt., *S. neglecta* T. & G., *S. uniligulata* (DC.) Porter, *S. humilis* Pursh (not *S. humilis* Mill.), *S. chrysolepis* Fern., and *S. Purshii* Porter, have had a very complex nomenclatorial history (12, 14, 16, 17). It is now generally agreed that there are two main types of plants in this complex: those with the secund heads and others with non-secund heads. Cronquist (12) has shown that ". . .the name *S. uliginosa* in the strict sense must apply to the secund plant. . .." He considers the secund and non-secund plants as varieties of one species, the former being the var. *uliginosa* and the latter the var. *peracuta* (Fern.) Friesn. A few months after Cronquist's publication, Fernald (16) insisted that he considered these two types as distinct species on account of their morphological differences, their ecological preferences, and their geographical distribution, and also referred the secund plants to *S. uliginosa* Nutt. but the non-secund plants to *S. chrysolepis* Fernald.

Two years later (17), however, he recognized that *S. Purshii* Porter was the correct name for the non-secund plants. We have determined the chromosome number of a large number of plants of this complex (Table II). Without exception, the non-secund plants have been found to possess 18 chromosomes in their root tips and the secund plants 36. It thus becomes certain that these two types of plants are characteristic of two different species as maintained by Fernald (16). However, as clearly pointed out by Cronquist (12), the position of the heads on the branches of the inflorescence is a somewhat variable character. In our experience, these two species of similar appearance can be separated with reasonable assurance only when they are in full bloom: it can then be seen that the inflorescence of *S. uliginosa* varies from a compact, oblong panicle to an open and triangular one, with a large number of their branches having clearly secund heads; that of *S. Purshii* is nearly always a characteristic thyrsus with non-secund heads. Moreover, in the region of Montreal, *S. Purshii* begins to bloom about one month before *S. uliginosa*.

Another group of closely similar entities is that constituted by *S. spathulata* DC. (*S. decumbens* Greene), *S. Randii* Porter, *S. racemosa* Greene, and *S. Gillmani* Steele. Cronquist (13) has grouped them all under one aggregate species in which these entities have been recognized as varieties. Our data, which concern only two of these entities, the eastern *S. Randii* and the western *S. spathulata* var. *neomexicana*, indicate that the first is tetraploid and the second diploid. More determinations are needed on the various elements of this baffling complex.

The gametic number of 9 reported by Goodwin (23) for 11 individuals of *S. rugosa* is confirmed by our somatic number of 18. This author has also determined a gametic number of 9 in two plants of *S. rugosa* var. *aspera*, one from Massachusetts and the other from Tennessee (Table I). Our gametic number of 9 and somatic of 18 also confirm the gametic number of 9 reported by the same author for 11 individuals of *S. sempervirens* from Nova Scotia and Massachusetts. In four individuals of *S. sempervirens* var. *mexicana* from Maryland and Florida, Goodwin (*loc. cit.*) has also reported a gametic number of 9, but in one individual of "*S. sempervirens*" from Fort Myers, Florida, i.e., within the range of var. *mexicana*, he has found a gametic number of 18.

The clearest subdivisions of *Solidago* are *Euthamia* and *Oligoneuron* which have been proposed as segregate genera, the first by Cassini (9) in 1825 and the second by Small (36) in 1903. Our data show that the basic chromosome number of some of their constituent species (*S. graminifolia* and *S. tenuifolia* for *Euthamia*, and *S. parvirigida*, *S. rigida*, and *S. Riddellii* for *Oligoneuron*) is the same as that of the other species of the genus, and consequently do not lend support to or contradict this segregation.

Summary and Conclusions

Thus far, only one basic number, nine, has been found in *Solidago*. From a total number of 42 taxa which have been studied to date 33 are diploid, 5 are tetraploid, 3 are aggregate since they contain both diploid and tetraploid

cytodemes, and 1 is hexaploid. If we calculate these statistics on the basis of species rather than taxa, out of 32 (excluding *S.* × *asperula*), 24 are diploid, 5 are tetraploid, 2 contain both diploid and tetraploid cytodemes, and 1 is hexaploid. Polyploidy has thus contributed to the evolution of the genus *Solidago* but it appears that most species have differentiated gradually.

The *S. decemflora* of De Candolle should be recognized as an entity specifically distinct from *S. nemoralis* since the two differ by their morphology, their geographical distribution, and their degree of ploidy, the first being tetraploid and the second diploid.

The *S. rigida* of authors is an aggregate constituted by two entities, one diploid and the other tetraploid, which are further differentiated by their morphology and their geographic range. The diploid one is smaller plant, of western distribution, and should be designated as *S. parvirigida*. The tetraploid is the large eastern plant, to which the binomial of Linnaeus, *S. rigida*, applies.

S. Purshii and *S. uliginosa* are also distinguished not only by their morphology and distribution but also by their chromosome numbers, the first being diploid and the second tetraploid.

S. graminifolia and *S. tenuifolia* of the section *Euthamia*, and *S. parvirigida*, *S. rigida*, and *S. Riddellii* of the section *Oligoneuron*, of the genus *Solidago*, have the same basic number as other species of the genus. This fact does not lend support to the segregation of these entities into separate genera. But chromosome numbers are not the only characters worth considering when such divisions are being made and other factors may exist which justify these separations.

Acknowledgments

The authors wish to thank the numerous botanists whose names have been listed earlier and who have helped them to obtain many of the plants on which they have worked; without them this study would have been much less detailed. Thanks are also extended to the authorities of the Montreal Botanical Garden for the generous facilities placed at our disposal, to Dr. Ernest Rouleau for his help on problems of nomenclature, to Miss Ingeborg Blume for her excellent technical assistance, and to the National Research Council of Canada for financial support. Dr. Ernest Rouleau, Dr. Åskell Löve, and Mr. Marcel Raymond, who have read the original manuscript, are cordially thanked for their suggestions.

Résumé

Les nombres chromosomiques de 25 taxa du genre *Solidago* sont rapportés pour la première fois. Une revue de la littérature révèle que nous connaissons maintenant les nombres chromosomiques de 42 des taxa de ce genre. Le nombre de base du genre *Solidago* est neuf. Trente-trois taxa sont diploïdes ($2n = 18$), cinq sont tétraploïdes ($2n = 36$), trois sont des complexes contenant deux cytodèmes, l'un diploïde et l'autre tétraploïde, et un est hexaploïde ($2n = 54$). La polyploïdie a donc participé à l'évolution du genre

Solidago mais il semble que la majorité des espèces se soient différenciées graduellement. Le *S. decemflora* DC. de l'ouest de l'Amérique du Nord diffère du *S. nemoralis* de l'est du même continent par des caractères morphologiques, par sa distribution géographique et son nombre chromosomique, le premier étant tétraploïde et le second diploïde; il s'agit donc là de deux bonnes espèces et non pas seulement de deux variétés d'une même espèce. Le *S. rigida* des auteurs est un complexe de deux entités qui diffèrent non seulement par leur morphologie et leur distribution géographique mais aussi par leurs nombres chromosomiques; l'unité orientale (*S. rigida* L.) est tétraploïde, alors que l'unité occidentale (*S. parvirigida* Beaudry) est diploïde. Les verges d'or des tourbières et des marécages, *S. Purshii* Porter et *S. uliginosa* Nutt., diffèrent aussi par leurs nombres chromosomiques, la première étant diploïde et la seconde tétraploïde.

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THE RELATION OF BARK MOISTURE TO THE DEVELOPMENT OF CANKER DISEASES CAUSED BY NATIVE, FACULTATIVE PARASITES

I. CRYPTODIAPORTHE CANKER ON WILLOW[1]

JOHN E. BIER[2]

Abstract

A close correlation was found to exist between the development of the willow bark canker, caused by *Cryptodiaporthe salicina* (Curr.) Weh., and the moisture content of the bark. When this was expressed as a percentage of the amount of water required to saturate the sample under experimental conditions, relative turgidities of 80% or more inhibited canker development which, however, occurred normally at lower percentages. Studies of the epidemiology of this disease in the Vancouver area afforded evidence in support of the limiting effect of bark moisture on canker development. Thus during the dormant season of 1957–58 the monthly average temperature was significantly higher than the minimum temperature for the growth of *C. salicina* on potato dextrose agar and the relative turgidity did not reach the inhibiting value of 80%. Cankers continued to develop throughout this period. During the growing season while temperatures were still more favorable for fungus development no extension of cankers occurred, apparently because, during the growing period, the relative turgidity was in excess of 80%. Canker development was prevented during the winter by placing dormant twigs in water, which likewise increased the moisture content of the bark above the 80% level.

Introduction

During the dormant seasons of 1956–57 and 1957–58 it was observed that mortality was occurring in young stems of willow (*Salix hookeriana* Benth. and *S. scouleriana* Barratt) in Vancouver as the result of stem cankers with the associated fungus *Cryptodiaporthe salicina* (Curr.) Weh. Further, an examination of the annual ring of wood beneath the lesions demonstrated that canker development had occurred after the end of the 1956 or the 1957 growing seasons. During the winter numerous cankers in an active, growing condition could be found on a single stem, the bark lesions originating at nodes, lenticels, and insect wounds (Figs. 1 and 2). A survey for cankers caused by facultative parasites on other hosts led to the general observation that this type of disease was more common in Vancouver than in areas examined in eastern Canada. It appeared that the moderate climate of Vancouver is favorable to the spread and growth of *C. salicina* during the winter when the bark tissues of the host are in a dormant condition. During the period September, 1956 to July, 1958, except for the months of December, 1956, and January, 1957, the monthly average temperatures were higher than the minimum (approximately 5° C) for the growth of *C. salicina* on potato dextrose agar.

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Contribution from the Department of Biology and Botany, and the Faculty of Forestry (Research Paper No. 25), University of British Columbia, Vancouver 8, British Columbia. Financial support for this project was granted by the National Research Council of Canada.
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Literature Review

Goidanich (5) and Wright (10) have outlined results on the greater intensity of canker diseases caused by facultative parasites on poplar of suboptimal vigor attributable to unfavorable climatic and/or soil influence. Mooi (6) in 1948 considered frost and wind to be factors predisposing willow to Cryptodiaporthe canker. In addition to predisposition of the host to this type of disease by climatic and/or soil maladjustment, mention has been made of a greater development of some of these diseases during the dormant season of the hosts. For example, Waterman (8) in 1957 reported as follows in connection with the susceptibility of poplar hybrids to Dothichiza canker: "This indicates that natural infection of twigs or branches may take place in the summer when the spores are discharged from the pycnidia, but the results of such infection will not be evident until the following growing season." Mooi's (6) inoculations of *C. salicina* on willow were positive when made in October and November and negative when made in April and July, indicating that susceptibility to the disease was limited to the dormant season of the host. Gibbs (4) has reported that the water content of willow bark is lower during the dormant period.

In much of the previous work one factor that appears in common is the possibility that the canker diseases developed, for the most part, when the bark tissues of the infected trees were low in moisture. The possibility of this relation has been recognized for many years. Münch (7) in 1909 reported that a reduction in the water supply of the cortex of elm led to a greater attack by *Nectria*. Other researchers have reported that disease resistance arising from a higher water content was due to a reduction in oxygen and/or biochemical changes in the host tissues. Reviews of this earlier work have been made by Gaümann (3) and Butin (2).

In 1955 Butin (2) reported on the relation between the water content of poplar and resistance or susceptibility to Cytospora canker. Laboratory experiments on cuttings demonstrated that canker development began when the total water content of the cuttings was reduced from 18% to 22%. A relation was found between water content and the formation of wound periderm. Viable host material low in water did not produce wound periderm and became susceptible to canker. It was concluded that wound periderm functioned as a barrier against the penetrating fungus.

Objectives of the Study

It is recognized that the basic cause or causes for resistance to the facultative parasites causing canker diseases may be very complex and involve water supply, oxygen supply, biochemical changes, and specific or non-specific reactions of the host to the pathogens. However, the water content of the host may be of primary importance in the initiation and degree of activity of many other phenomena.

Generalizations from the results of studies correlating the incidence and intensity of such a disease as Cryptodiaporthe canker with seasonal, climatic, or soil factors are difficult, since many of the interrelated factors vary considerably on a local as well as on a regional basis. Further, a consideration of such results frequently leads to a number of multiple correlations whose relative significance is most difficult to assess. The expression of disease vulnerability on a basis of the moisture content of the bark tissues of the host may be of general application, since at one time and place the water content of the bark would serve as a direct expression of the interaction of the many seasonal, climatic, and soil factors which influence tree growth and vigor.

This paper outlines the results of laboratory experiments designed to determine the relation between the water content of viable willow bark and the development of Cryptodiaporthe canker. The laboratory experiments relate to bark moisture and disease development studies conducted in the field during the periods of dormancy and active growth.

Methods of Investigation

Bark Moisture Determinations

In 1957 the development of natural and artificially induced cankers was related to bark moisture, expressed as the percentage of the amount of water in a bark sample to the fresh weight or to the dry weight of the same bark sample (1). Studies of individual cuttings demonstrated a relation between bark moisture and canker development when bark moisture was expressed in this way. However, it was not possible to so relate bark moisture and canker development in different cuttings from one stem or tree because of such factors as variation in the density of the bark tissues.

Because of this a different method of expressing bark moisture was sought which might exclude factors related to varying specific gravity among the samples. Experiments indicated that measuring water on a basis of the relative turgidity of the bark tissues would overcome the difficulties mentioned. Relative turgidity of bark tissues, as used in this work, is the initial amount of water in the sample expressed as a percentage of the water present in the same bark tissues when completely saturated. In 1950 Weatherley (9) reported that a determination of the relative turgidity of leaf samples provided a suitable method for investigating the water relations of the cotton plant.

A sharp cork borer and scalpel were used to excise and remove samples of the bark to the cambium. Determinations were made of the fresh weights of the samples. The bark disks were then transferred to sterilized water and allowed to soak until saturated with water and constant weights were obtained. After a number of weighings it was decided to soak all bark samples for a uniform period of 24 hours, and the saturated bark samples were weighed after the surface water had been removed with blotting paper. The samples were then oven-dried and weighed again. The three weighings provided data for

determining the amount of water in a fresh sample and the amount of water required to saturate the same bark sample. The percentage relative turgidity is expressed as follows:

$$\frac{\text{weight of water in a bark sample} \times 100}{\text{weight of water required to saturate the same sample}}.$$

It is recognized that some leaching of the bark would occur when the samples were placed in distilled water, which would affect the absolute values for bark moisture. However, the objective in this study was the determination of comparative, rather than absolute, values. This relative turgidity value appeared to provide an expression of the existing amount of moisture relative to the maximum capacity of the bark to absorb moisture. This was not affected by factors as differences in bark density.

Methods of Inoculation

In the outdoor inoculations wounds were made by scorching an area of healthy bark with a hot scalpel. A portion of agar with actively growing mycelium from a multispore culture of *C. salicina* was placed on the wound. The inoculum was kept moist during the period of incubation by placing moist cotton above and below the wound and covering with wax paper or Saran Wrap. The incubation period lasted approximately one month.

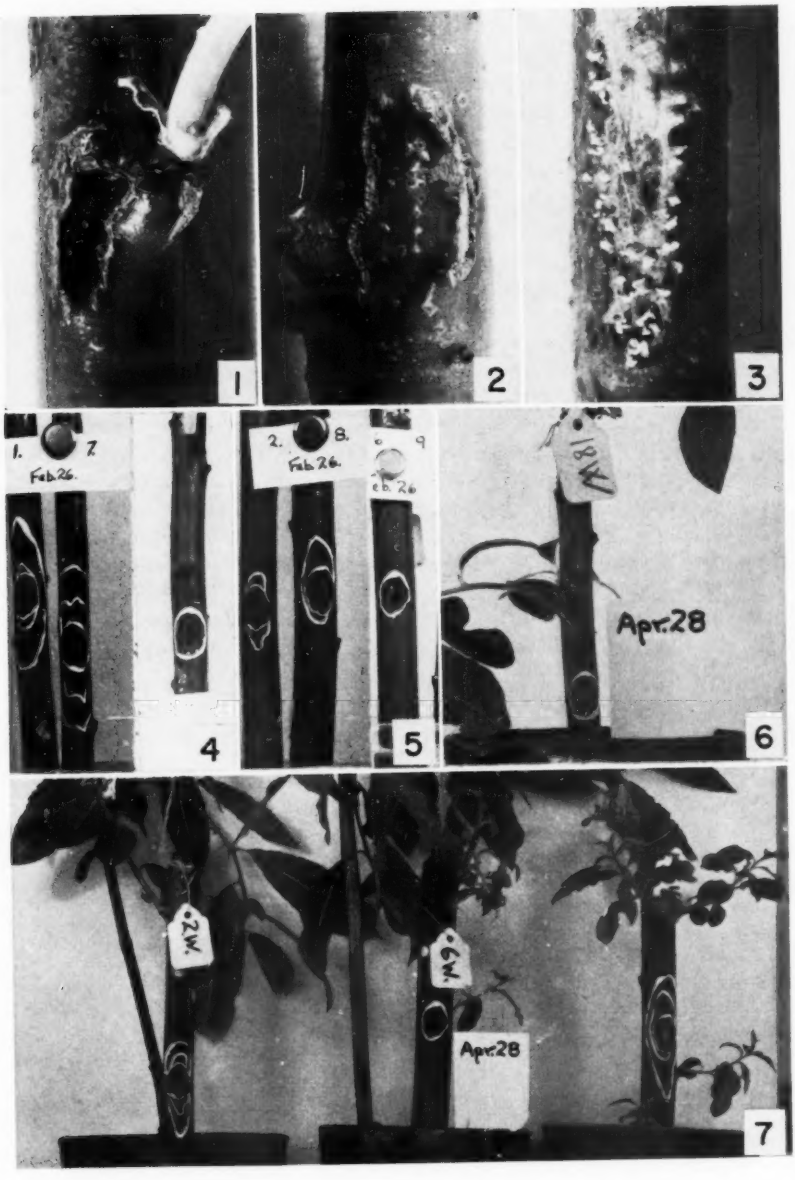
In the laboratory inoculations, burned wounds were made in the same manner as for the outdoor inoculations. The portion of agar containing mycelium was held in position on the wound with Scotch tape. The inoculated cuttings were incubated in a moist chamber in the laboratory at room temperature for a period of approximately two weeks.

Controls were prepared in the same manner as the inoculations with the exception that the fungus was not placed on the wounds.

Experimental Results

The experiments outlined are representative of many which have been investigated to determine the correlation between the relative turgidity of the bark and 1- and 2-year-old willow plants and the development of Cryptodiaporthe canker. The water/dry weight values for bark moisture were also determined. All of the cuttings used in these experiments originated from one root system in order to eliminate genetic variation in the host material.

FIG. 1. Nodal infection of *C. salicina* on willow.
FIG. 2. Lenticel infection of *C. salicina* on willow.
FIG. 3. Imperfect stage (*D. carbonacea*) on canker resulting from an artificial inoculation.
FIG. 4. Cankers and control on dormant cuttings allowed to dry outdoors for a period of 56 days after inoculation. Middle white lines show the canker growth after a 38-day period of drying.
FIG. 5. Cankers and control on dormant cuttings placed outdoors; water withheld for 38 days after inoculation and supplied for 18 days.
FIG. 6. Control cutting illustrated in Fig. 4; water withheld for 56 days.
FIG. 7. Cankers and control on cuttings illustrated in Fig. 5; water withheld for 38 days and supplied for 74 days.



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The cuttings were taken from the basal half of the major 1- and 2-year-old shoots since such material was most likely to survive.

Many fructifications of *Discella carbonacea* Berk. and Br., the imperfect stage of *C. salicina*, developed on the cankers in less than two months after inoculation (Fig. 3). Isolations from the conidia and infected bark yielded cultures identical with those used for inoculum.

Dormant Cuttings Inoculated and Subjected to a Period of Dry, Winter Storage

In this experiment 24 dormant cuttings were collected in the university area, Vancouver, on January 6, 1958. The ends of the cuttings were sealed with lacquer to prevent rapid drying. Twenty cuttings were inoculated and four served as controls. After treatment the cuttings were placed outdoors in a wire basket. On February 13, after a 38-day period of drying, fresh cuts were made on the basal ends of 13 inoculated and 2 control cuttings which were then placed outdoors in a beaker containing distilled water to a depth of approximately one inch. A continuous supply of water was provided. The remainder of the cuttings were allowed to dry for a longer period. On March 3, 56 days after treatment, the cuttings in water outdoors were planted in the laboratory in pots which were then placed in shallow, metal trays provided with a continuous supply of water. The results of this experiment may be summarized as follows:

1. The burned wounds killed an average of 23% of the circumference of the cuttings (Fig. 8).

2. The field measurement of bark moisture on January 6 gave an average water/dry weight value of 125%, and an average relative turgidity value of 79% (Fig. 8).

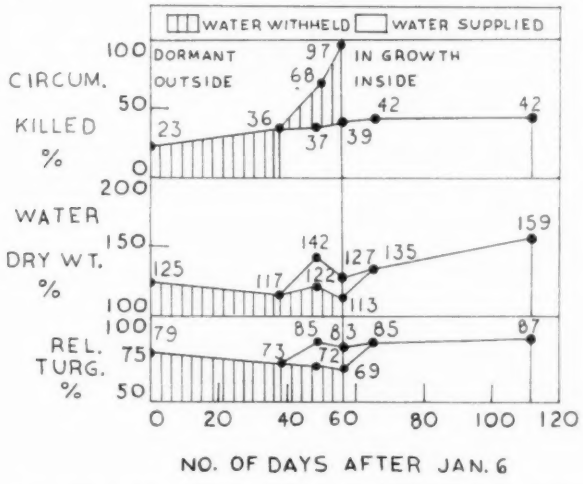


FIG. 8. The relation of bark moisture to the development of Cryptodiaporthe canker in dormant cuttings inoculated and subjected to a period of dry, winter storage.

3. After a 38-day period of dry storage outdoors the average values for bark moisture in the dormant cuttings were water/dry weight 117%, and relative turgidity 73%. Canker development occurred and an average of 36% of the circumference of the inoculated cuttings had been killed. Canker development did not occur in the control cuttings (Figs. 5 and 8).

4. *C. salicina* girdled and killed the dormant cuttings allowed to dry outdoors until March 3, 56 days after inoculation. After this period of drying, the average bark moisture readings were water/dry weight 113%, and relative turgidity 69%. Bark lesions did not develop on the control cuttings, which developed into healthy trees when planted in the laboratory (Figs. 4, 6, and 8). Therefore, cuttings allowed to dry for this period retained their vitality.

5. No canker development occurred after the dormant cuttings were placed outdoors with their basal ends in water. On March 3, 13 days after water was supplied, the average bark moisture readings were water/dry weight 127%, and relative turgidity 83% (Figs. 5 and 8). By April 28, 74 days after water was supplied, the inoculated and control cuttings had developed into healthy trees (Fig. 7). At this time the average values of bark moisture for all cuttings were water/dry weight 159%, and relative turgidity 87% (Fig. 8). Some canker growth, primarily in a longitudinal direction, occurred shortly after the inoculated cuttings were planted (Fig. 7). It was evident that shoot development occurred before root development and this resulted in a period of moisture stress.

6. During the summer of 1958 normal growth occurred in the cuttings without further advance of the fungus in the bark tissues. By September 1, the host had produced wound periderm around the margin of the lesions.

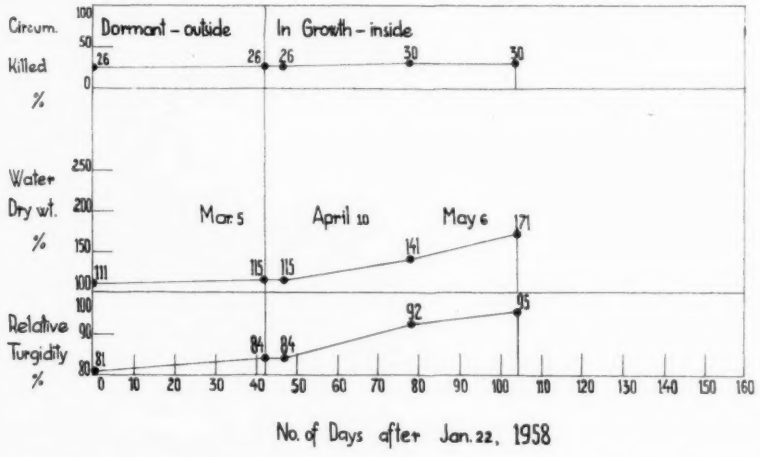


FIG. 9. The relation of bark moisture to the development of Cryptodiaporthe canker in dormant cuttings inoculated and provided with a continuous supply of water.

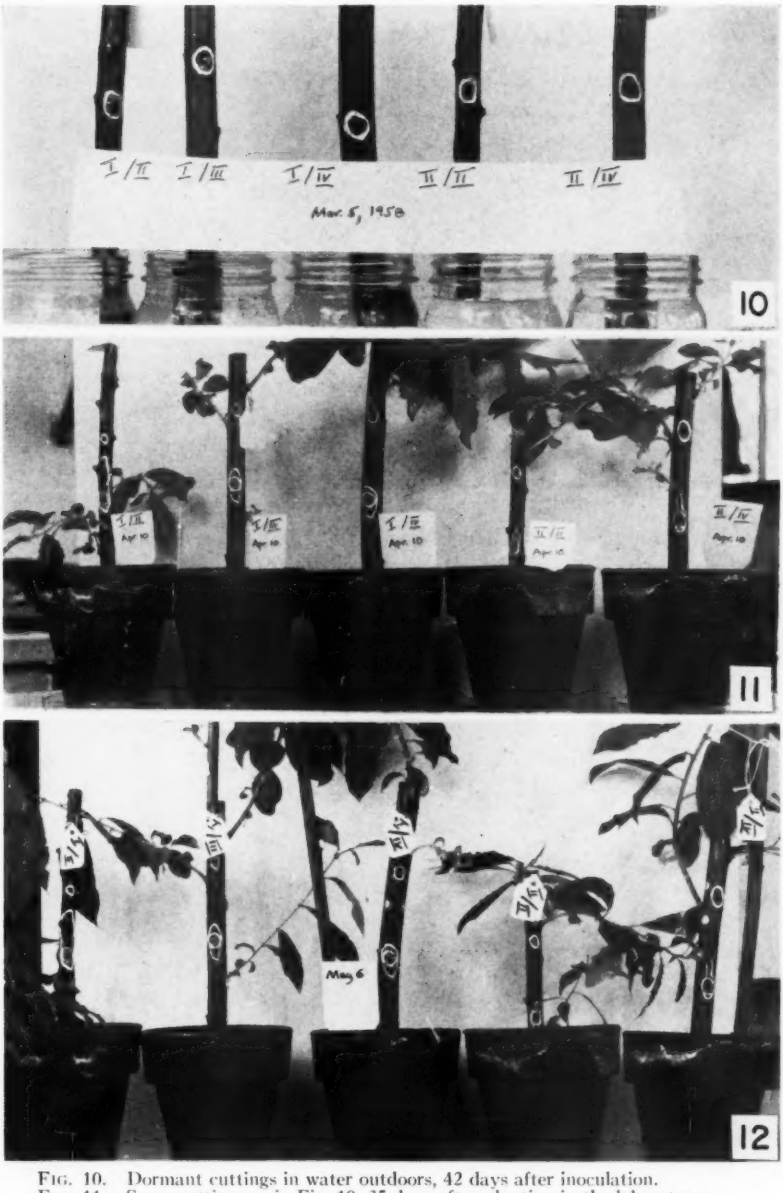
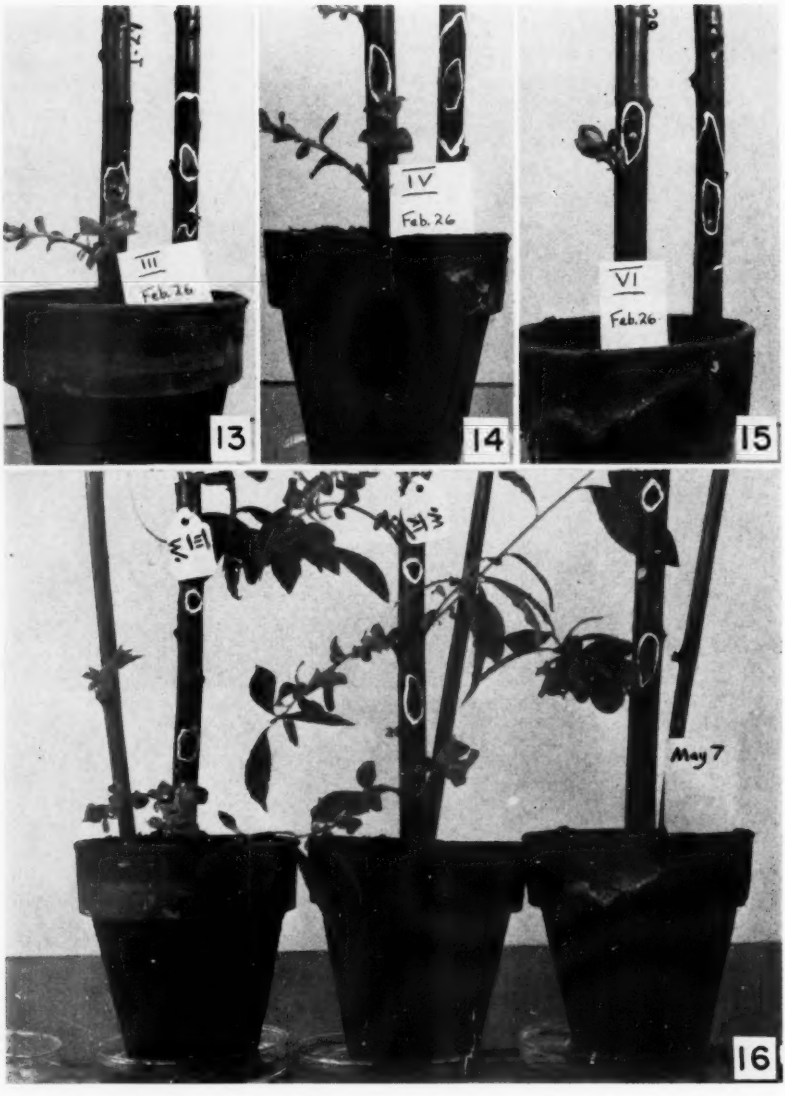


FIG. 10. Dormant cuttings in water outdoors, 42 days after inoculation.
FIG. 11. Same cuttings as in Fig. 10, 35 days after planting in the laboratory.
FIG. 12. Same cuttings as in Fig. 11, 62 days after planting in the laboratory.



FIGS. 13, 14, and 15. Left member of each pair, water withheld for 18 days and supplied for 9 days. Right member of each pair, water withheld for 27 days. The inner white lines show the canker development 18 days after inoculation.

FIG. 16. Same cuttings as on the left of Figs. 14, 15, 16; 70 days after planting in the laboratory.

Dormant Cuttings Inoculated and Provided with a Continuous Supply of Water

Five dormant cuttings were collected on January 22, 1958, and placed in a beaker containing distilled water. One inoculation and a control injury were made on each cutting. After treatment the cuttings were placed outdoors with their basal ends in water until March 5, a period of 42 days. The dormant cuttings were then planted in the laboratory in pots placed in a shallow, metal tray provided with a continuous supply of water. The results of this experiment may be summarized as follows:

1. The burned wounds killed an average of 26% of the circumference of the cuttings (Fig. 9).

2. The field measurement of bark moisture on January 22 gave an average water/dry weight value of 111%, and an average relative turgidity value of 81% (Fig. 9).

3. After a 42-day period of storage outdoors with water supplied, the average values for bark moisture of the dormant cuttings were water/dry weight 115%, and relative turgidity 84%. Canker growth did not occur during this period. In this instance active growth of the host was not required to prevent the development of the disease (Figs. 9 and 10).

4. By May 6, 62 days after planting, the cuttings had developed into healthy trees (Fig. 12). The average values for bark moisture were water/dry weight 171%, and relative turgidity 95% (Fig. 9). A little canker development occurred shortly after the cuttings were planted (Fig. 11). It is believed that this was correlated with a period of moisture stress which occurs prior to the formation of root systems. Bark lesions did not develop on the control wounds.

5. During the summer of 1958 normal growth occurred in the cuttings without further advance of the fungus in the bark tissues. By September 1, 179 days after planting, wound periderm was present at the margin of the diseased areas.

6. Canker development did not occur in bark tissues with a relative turgidity above 80%, which appears to confirm the results obtained in the previous experiment.

Dormant Cuttings Inoculated and Subjected to a Period of Drying in the Laboratory

Sixteen cuttings were collected on January 30, 1958. The ends of the cuttings were sealed with lacquer to prevent rapid drying. One inoculation and a control wound were made on each cutting after which they were placed in a moist chamber in the laboratory. On February 17, 18 days after inoculation, eight cuttings were removed from the moist chamber, and, after making fresh cuts at the basal ends, were planted in pots that were placed in a shallow, metal tray provided with a continuous supply of water. The other eight cuttings were left in the moist chamber until February 26, or 27 days after inoculation. The results of this experiment may be summarized as follows:

1. The burned wounds killed an average of 23% of the circumference of the cuttings.

2. The field measurement of bark moisture on January 30 gave an average water/dry weight value of 112%, and an average relative turgidity value of 78% (Fig. 17).

3. After the cuttings were in the moist chamber for a period of 18 days the average values for bark moisture were water/dry weight 178%, and relative turgidity 72% (Fig. 17). This result in addition to others obtained in 1957 demonstrated the large increase in the water/dry weight percentage of the bark that occurs when dormant cuttings break into new growth. Canker growth occurred during this period, which appears inconsistent with the thesis that disease development does not occur in bark with high moisture. However, it is important to observe that an appreciable reduction in relative turgidity coincided with this increase in water/dry weight. The drop in relative turgidity conforms with the behavior of the fungus in the bark tissues.

4. *C. salicina* continued to girdle and kill the cuttings in the moist chamber until February 26, which was 27 days after inoculation. At this time the average bark moisture values were water/dry weight 88%, and relative turgidity 52% (Fig. 17).

5. Further canker development did not occur in the cuttings that were provided with water after an 18-day period of drying (Figs. 13, 14, and 15). Limited canker development occurred shortly after the cuttings were planted. As in the previous experiments, the fungous attack occurred from the time of planting until root systems had developed. On May 7, 70 days after planting, the bark moisture values were water/dry weight 174%, and relative turgidity 84% (Figs. 16 and 17).

6. During the summer of 1958 normal growth occurred in the cuttings without further advance of the fungus in the bark tissues. On September 1, 186 days after planting, wound periderm was present at the margin of the diseased areas.

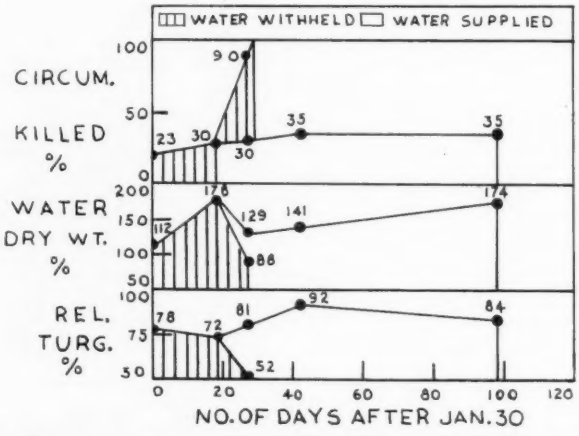


FIG. 17. The relation of bark moisture to the development of Cryptodiaporthe canker in dormant cuttings inoculated and subjected to a period of drying in the laboratory.

The Relation of Bark Moisture to the Development of Cryptodiaporthe Canker in the Field

Water/dry weight and relative turgidity values for willow bark in the field are given in Fig. 18. It is noted that during the months of January and February, 1958, the relative turgidity values fell below 80%. During this period canker growth occurred in the field. This conforms with the results of the inoculation experiments which demonstrated that the fungus attacks viable bark tissues with a relative turgidity below 80%. A considerable increase in the relative turgidity of the bark occurs with the breaking of dormancy, and this increase was maintained throughout the growing season (Fig. 18). From May to September, 1958, the relative turgidity values varied between 85% and 95%. This increase in bark moisture coincided with a cessation of canker growth in the field, and the production of wound periderm around the margin of lesions which is now delimiting the diseased areas. The cessation of canker growth in bark tissues with a relative turgidity above 80% agrees with the results of the laboratory experiments.

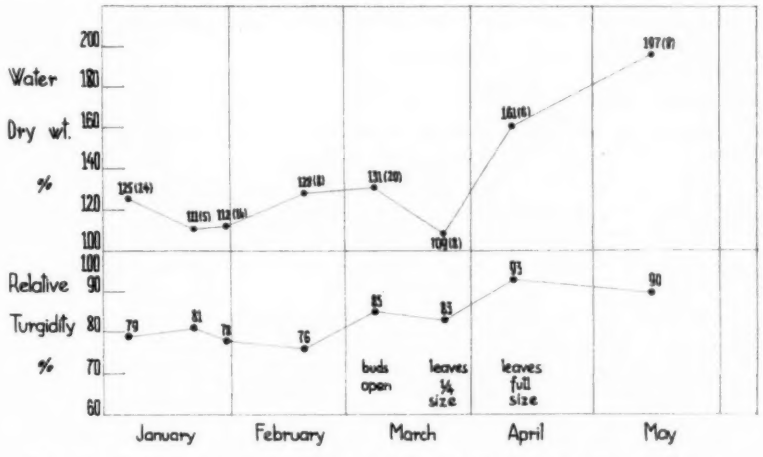


FIG. 18. Field measurements of bark moisture obtained from willow in Vancouver, 1958.

Discussion and Summary

Laboratory and field experiments have shown a correlation between the relative turgidity of willow bark and the development of Cryptodiaporthe canker, the fungus invading bark tissues only when the relative turgidity was below 80%. No canker development occurred in bark with a relative turgidity above 80%. Therefore, subsequent to artificial inoculation or natural infection the disease may develop or be suppressed depending on the condition of the living host bark as indicated by its relative turgidity. This relation

between the relative turgidity of willow bark and the development of Cryptodiaporthe canker suggests the possibility of using relative turgidity values as indices of the susceptibility or resistance of cuttings, seedlings, and larger trees to this disease.

Dormant willow cuttings inoculated with *C. salicina* and placed outdoors during the winter with their basal ends in water maintained relative turgidity values above 80%, and there was no development of canker. In this instance the host did not have to be actively growing to prevent the fungus from invading the living bark. On drying, the relative turgidity of the experimental material could be reduced to 69% without the cuttings losing their vitality.

During the dormant season the relative turgidity of the bark of field willows was found to fall below 80% and thus they are susceptible to Cryptodiaporthe canker. Relative turgidity values of the bark during the growing season, on the contrary, are above 80%, which indicates it should be resistant to the disease. Studies on the development of the disease in the field agree with these findings. The winter of 1957–58 in Vancouver was very moderate and free from periods of extreme temperature change which would bring about excessive drying in the bark tissues and the minimum relative turgidity value obtained was 76%. During a more severe winter the relative turgidity of the bark might well fall below that value.

A similar relation between the relative turgidity of the bark and disease development has been found for a canker disease on *Populus trichocarpa* Torrey and Gray caused by *Fusarium lateritium* Nees. The results of this investigation will be published in a separate paper.

Attention is directed to the possible importance of maintaining a satisfactory level of relative turgidity in the bark of trees and cutting stock as a cultural method designed to prevent canker diseases caused by facultative parasites.

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EFFECT OF BENZIMIDAZOLE, DIMETHYLBENZIMIDAZOLE, GLUCOSE, AND METAL IONS ON THE DEVELOPMENT OF PUCCINIA GRAMINIS TRITICI ON DETACHED LEAVES OF KHAPLI WHEAT[1]

DALTON WANG[2]

Abstract

Leaves of Khapli wheat which are normally resistant to race 15B-1 of *Puccinia graminis tritici* become susceptible when detached and floated on water. This breakdown of resistance can be reversed by floating the detached leaves on a solution of benzimidazole. The effect of benzimidazole, however, can be nullified by a supply of exogenous glucose or 5,6-dimethylbenzimidazole. Furthermore, the resistance can again be restored by the presence of cobalt ion combined in solution with glucose and benzimidazole or with glucose and 5,6-dimethylbenzimidazole. Cobalt ions alone, or in combination with glucose, or with benzimidazole, or with 5,6-dimethylbenzimidazole separately have no effect on rust development. In contrast, nickel ion alone or in any combination has a profound inhibitory effect on the development of rust in detached leaves. Other chemicals were also included in this study, and their effect on rust development is discussed. It is speculated that benzimidazole or a derivative of it and cobalt may form a vitamin B_{12}-like factor which is required by the host to maintain its normal metabolic activities.

Introduction

Benzimidazole has been investigated by various workers for its action in biological systems as an antagonist of purine compounds (5, 6, 7, 8, 14). Recently, Person *et al.* (9) reported that benzimidazole can prolong considerably the life span of detached wheat leaves. It has been shown that with appropriate concentrations of benzimidazole the original rust reaction of the attached Khapli leaf could be retained and that an exogenous supply of glucose could modify the effect of benzimidazole on rust development in the detached leaves of Khapli (10).

In the present investigation, an attempt has been made to elucidate the possible role of benzimidazole in the host–parasite relation, and the mechanism of the inactivation of benzimidazole brought about by glucose. This paper describes some of the results which led to the speculation of the involvement of a vitamin B_{12}-like factor in the host.

Methods

The first leaves of Khapli seedlings were inoculated at the two-leaf stage with urediospores of *Puccinia graminis tritici* (race 15B-1) and incubated for 24 hours in a moist chamber. At the end of incubation, the inoculated leaves

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were excised and floated on 20 ml of water or on various solutions in Petri plates. Petri plates containing the excised leaves were then placed in a growth chamber (21° C) and subjected to a light period (650 ft-c) of 8 hours daily. The development of rust was noted on the eighth or ninth day.

Six first leaves of Khapli seedlings were excised at the two-leaf stage and cut into approximately 0.5 cm long sections. They were infiltrated under vacuum with either sterile tap water or 0.05 *M* phosphate buffer (pH 7), blotted, and subsequently placed in small Petri plates containing 2 ml of either a solution of benzimidazole (50 p.p.m.) and 0.37 mg (2.5 μc) of glucose-U-C^{14} or a similar solution with no benzimidazole. The Petri plates were placed in a growth chamber in light for a period of 2, 3, or 24 hours. At the end of each incubation the leaf sections were removed, washed thoroughly with distilled water, and killed rapidly in 15 ml of boiling 80% ethanol. The tissues were refluxed for 30 minutes with 15 ml of 80% ethanol which was followed by a second extraction with 40% ethanol. The extracts were combined, evaporated, and dissolved in 1.0 ml 80% ethanol. Ascending two-dimensional chromatograms using 150 μl aliquots were made on Whatman No. 1 paper with phenol:water (80:20) and butanol:acetic acid:water (4:1:5) as solvents. Radioautograms were prepared from these chromatograms.

Results

Effect of Different Concentrations of Benzimidazole and Glucose on Rust Development

Leaves of Khapli wheat, normally resistant to race 15B-1 of *Puccinia graminis tritici*, become susceptible after detachment when floated on water. It was found that the rust reaction characteristic of the attached leaves of Khapli could be restored by floating the detached leaves on a solution of 40 p.p.m. of benzimidazole, but that this effect could be nullified by an exogenous supply of glucose (1% or more). These results confirmed the findings of Samborski *et al.* (10). However, under these experimental conditions, the glucose effect (1%) could not be overcome by an increased benzimidazole concentration (60 p.p.m.) as reported by the above workers. With 80 p.p.m. benzimidazole, results varied considerably. Even with 100 p.p.m., benzimidazole occasionally failed to overcome the 1% glucose effect.

When the concentration of glucose was increased from 1 to 3% while maintaining benzimidazole at 40 p.p.m., no corresponding increase in either sporulation or rate of rust development in the detached leaves was observed.

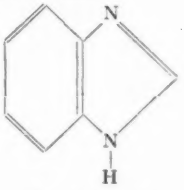
Spore germination tests showed that benzimidazole at 50 p.p.m. had no effect on either germination of the spores or the growth of their germ tubes.

Effect of 5,6-Dimethylbenzimidazole on Benzimidazole

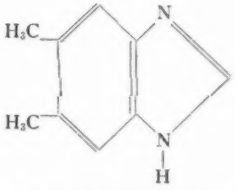
Several substances structurally related to benzimidazole occur naturally in biological systems. A derivative of this compound 5,6-dimethylbenzimidazole (see below) constitutes a part of a vitamin B_{12} molecule. However, vitamin B_{12} has not been reported to be required by higher plants. It would appear

logical that substances that might act as antagonists of benzimidazole would also influence rust development in the detached Khapli leaves.

When 5,6-dimethylbenzimidazole was added at 20 p.p.m. to a solution of benzimidazole at 20, 30, or 40 p.p.m., it showed the same effect on rust development as when glucose was combined with the latter. The effectiveness of this compound in overcoming the benzimidazole effect was somewhat less than that of glucose.



Benzimidazole



5,6-Dimethylbenzimidazole

Effect of Metal Ions in Overcoming the Glucose Effect

No correlation could be observed between increasing concentrations of benzimidazole and the extent to which it overcomes the effect of glucose, and this suggests that there might be other factors that become limiting in the presence of glucose. Cobalt ion was the first tested owing to its prominent position in the vitamin B_{12} molecule. It was found that the effect of glucose on benzimidazole was completely eliminated by 2 p.p.m. of cobalt ion. The range of effective concentration of this metal ion was found to be 0.5 to 4 p.p.m. Concentrations of cobalt above 4.0 p.p.m. were extremely toxic to the detached leaves. Furthermore, it was found that 2 p.p.m of cobalt ion was also capable of overcoming the 5,6-dimethylbenzimidazole effect on benzimidazole. These experiments suggest that glucose and 5,6-dimethylbenzimidazole compete with benzimidazole for the cobalt ion.

In order to test the specificity of the metal ion requirement of this system on the reversal of the glucose effect on benzimidazole, the following metal ions, Ni^{++}, Zn^{++}, Mo^{++}, Cu^{++}, Mn^{++}, and Fe^{++}, were tested. It was found that the last four metal ions were ineffective at concentrations up to 10 p.p.m. Zinc ion at 5 p.p.m. was quite effective in overcoming the effect of glucose, but not that of 5,6-dimethylbenzimidazole. The results with zinc ion, however, varied considerably. On the other hand, nickel ion yielded consistent results and was found to be markedly effective, even at a concentration as low as 0.5 p.p.m., in overcoming the effect of both glucose and 5,6-dimethylbenzimidazole. However, nickel ion alone, but not cobalt, is capable of checking the development of rust in detached leaves. This has already been reported by Wang *et al.* (13).

Effect of Ribose on Benzimidazole

When glucose was replaced by ribose, the latter did not show the same effect on benzimidazole-treated leaves. Ribose alone had no apparent effect on the development of rust, nor had glucose, but the former sugar diminished the toxic effect of cobalt ion (6 p.p.m.) when used with benzimidazole.

Effect of Pyridoxal Phosphate on Cobalt Ion

Pyridoxal phosphate, which is a codecarboxylase and also a cofactor in the process of transamination, either alone or in combination with glucose, or benzimidazole, or both, had no effect on rust development. However, it did accentuate the effect of cobalt ion in overcoming the effect of glucose on benzimidazole. Cobalt ion at concentrations of 2 to 4 p.p.m. often induced a relatively earlier chlorosis in the detached leaves as compared with those on water. But the chlorosis induced by 1×10^{-5} *M* cobalt ion was markedly decreased by 2×10^{-5} *M* of pyridoxal phosphate.

Biosynthesis of Glucose-U-C^{14}-Labelled Glucoside

No biosynthesis of glucoside was evident from these experiments in as much as the metabolic patterns of glucose-U-C^{14} in benzimidazole-treated leaves and in controls were qualitatively identical as indicated by the alcohol-extractable carbon-14-labelled compounds.

Discussion

Khapli leaf, normally resistant to race 15B-1 of *Puccinia graminis tritici*, becomes susceptible when detached and floated on water. This breakdown of resistance can be reversed by floating the detached leaves on a solution of benzimidazole. Furthermore, the effect of benzimidazole can easily be negated by a supply of exogenous glucose or 5,6-dimethylbenzimidazole. The mode of action of these two compounds is likely quite different. 5,6-Dimethylbenzimidazole, which is a derivative of benzimidazole, may act as an antagonist. But, the interaction between benzimidazole and glucose is more puzzling. It was thought that glucose may form a glucoside in lieu of a riboside with benzimidazole. The inability of ribose to replace glucose seems to lend some weight to the possibility of the formation of a glucoside. However, there is no direct evidence to support this hypothesis. The failure of detection of glucoside cannot, however, entirely rule out the possibility of glucoside formation, at least not until long-term experiments or similar experiments with rust-infected leaves are carried out.

Since exogenous glucose nullifies the effect of benzimidazole, a reversal of glucose effect may be expected if the concentration of benzimidazole is increased. The lack of a close correlation between the effectiveness of increasing concentration of benzimidazole in overcoming the glucose effect points to the possibility of an involvement of other factor or factors. The efficiency of the cobalt ion in overcoming the glucose effect strongly suggests that glucose competes with benzimidazole for this ion. The fact that cobalt ion induced chlorosis in the detached leaves indicates the possibility of an involvement of a factor or factors other than cobalt ion for completely restoring the effect of benzimidazole in the glucose-treated detached leaves. Among the metal ions tested, only those of zinc and nickel are effective. Their modes of action may be very different from that of cobalt ion, since nickel ion is extremely effective by itself

in the prevention of rust development (13), while zinc is ineffective in overcoming the effect of 5,6-dimethylbenzimidazole. Neither one of these two metal ions induces chlorosis to the same degree as does the cobalt ion: in fact, nickel has a preservative effect on the green pigments of the detached leaves (to be published). The cobalt-induced chlorosis can, however, be greatly reduced by pyridoxal phosphate. Moreover, pyridoxal phosphate accentuates the effectiveness of the cobalt ion in overcoming the glucose effect. On the other hand, both the cobalt-induced chlorosis and its toxic effect on the detached leaves are markedly diminished by an exogenous supply of ribose. The nature of the synergistic effect between pyridoxal phosphate and cobalt ion, and the action of pyridoxal phosphate and ribose on the reduction of cobalt-induced chlorosis, are not yet clear.

It is apparent that benzimidazole requires cobalt ion in maintaining the resistant state in the detached Khapli leaves. Cobalt and 5,6-dimethylbenzimidazole constitute two major components of a vitamin B_{12} molecule. However, no higher plant has yet been demonstrated to require vitamin B_{12}. Yet, several articles (2) have indicated the occurrence of vitamin B_{12} in higher plant tissues, but its origin is still disputed. Darken (2) comments that there is no unequivocal evidence for the synthesis of vitamin B_{12} within plant tissues. The various vitamin B_{12} molecules isolated from microorganisms differ from one another in their benzimidazole derivative only, e.g. 5,6-dimethylbenzimidazole occurs in one and adenine in another (4). As a result, they possess different biological specificities, i.e. one vitamin B_{12} may be required by one organism, but not by another. Since methods used for the detection of vitamin B_{12} are based on microbiological assays, it is possible that the vitamin B_{12} of higher plants, if there is any, may not be detected. It is not unreasonable to speculate that benzimidazole or a derivative of it and cobalt may form a vitamin B_{12}-like factor which is required by the host (in this case, the detached leaf) to maintain its normal metabolic activities.

It has been shown in this laboratory that when glucose-U-C^{14} is fed to leaves, benzimidazole increases the radioactivity of the hot trichloroacetic acid (TCA) fraction (nucleic acid) of the leaf tissue from 40 to 60% of the control, whereas no increase in radioactivity has been found in cold TCA and protein fractions (unpublished data). In a long-term experiment, Samborski *et al.* (10) showed a stimulating effect of benzimidazole on protein synthesis. These findings would lend indirect support to the above hypothesis, since vitamin B_{12} has been reported to mediate both nucleic acid and protein metabolism in animal tissues and microorganisms (1, 3, 11, 12).

Acknowledgments

The author is grateful to Dr. E. R. Waygood, Head of the Department of Botany, University of Manitoba, Winnipeg, Manitoba, for his helpful criticism of the manuscript.

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STUDIES ON FUSARIUM WILT OF BANANAS

IV. CLONAL DIFFERENTIATION AMONG WILD TYPE ISOLATES OF F. OXYSPORUM f. CUBENSE[1]

R. H. STOVER

Abstract

F. oxysporum f. *cubense* exists in diseased rhizomes and pseudostems of Gros Michel bananas in two major clonal groups or cultivars designated 'Odoratum' and 'Inodoratum' because of the presence or absence of a pronounced distinctive odor from cultures after 4 to 8 days on various media. Three clones of the 'Inodoratum' cultivar, difficult to distinguish morphologically on peptone dextrose agar, were distinguishable by cultural interaction and pathogenicity tests in the field. Some clones of the 'Inodoratum' and 'Odoratum' cultivars were shown to differ quantitatively in pathogenicity in the field. Clone C from Honduras, which is limited in distribution, induced the most rapid disease spread and destruction of banana mats, followed by clone E from Panama. There was an association between the 'Inodoratum' and 'Odoratum' cultivars and the syndromes induced in Honduras. The former usually induced strong yellowing of erect leaves whereas the latter usually induced leaf collapse at the petiole with little or no leaf yellowing.

Introduction

While isolations from banana rhizomes and pseudostems infected with *Fusarium oxysporum* f. *cubense* (E.F.S.) Sny. and Hans. were being made, several consistent morphological differences between isolates were observed. Since these differences might also reflect variation in pathogenic potential and disease behavior in the field, the most commonly occurring and distinctive isolates were chosen for description and study in culture. Concurrently, studies on their pathogenic potential in the field were begun.

Brandes (1) noted in 1919 that isolates of *F. oxysporum* f. *cubense* possessed or lacked an aromatic odor, similar to that of some of the aldehydes of the aliphatic series, when grown on steamed rice and certain liquid media. The odor was present or absent in cultures from Cuba and present in all cultures obtained in Panama, Costa Rica, and Jamaica. Brandes proposed the designation of "*Fusarium cubense* var. *inodoratum* n.v." for the odorless isolates from Cuba.

Hansford (2) recognized variability among naturally occurring isolates of *F. oxysporum* f. *cubense*. On the basis of morphological characteristics, he was able to obtain five distinct groups among several hundred isolations. He showed that these pathogenic groups were morphologically indistinguishable from saprophytic isolates of *F. oxysporum*.

Ward (12) recognized that differences existed among isolates from diseased bananas from various geographic locations in Malaya. He undertook pathogenicity studies, the results of which were not conclusive.

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Contribution from the Plant Pathology Department, Vining C. Dunlap Laboratories, Tela Railroad Co., La Lima, Honduras (a subsidiary of the United Fruit Co.).

Wardlaw (13) studied differences in cultural characteristics of five distinct "strains" of *F. oxysporum* f. *cubense*. From the description of his techniques, however, it is not clear whether he was describing cultural mutants or wild types (3).

Stover (10) found that two morphologically distinct isolates of *F. oxysporum* f. *cubense* were associated with two different syndromes in Honduras designated yellow and non-yellow. These isolates behaved differently in culture (11). Additional studies with these and other wild type isolates are reported in this paper.

Methods

A 6- to 12-in. portion of a *Fusarium*-infected Gros Michel pseudostem or rhizome was brought to the laboratory where approximately 50 g of discolored vascular tissue was dissected out, blended in a Waring blendor, and dilution plates made (8). Plates were poured with peptone dextrose agar containing rose bengal and streptomycin. This technique (8) assured ready dispersal of fungal particles on the plates, formation of discrete colonies, and the detection of morphological variability.

The terminology adopted for the classification of the isolates is based in part on that of Snyder and Hansen (6) and Stakman and Harrar (7) and is as follows:

Isolate: a culture of *F. oxysporum* f. *cubense* obtained from any source and non-classified as to clone or race.

Clone (biotype): isolates with the same genotype which are distinguishable from others on the basis of morphological and/or physiological traits including pathogenicity.

Cultivar: a distinct group of isolates that have some common morphological or physiological characteristics but which may consist of one or more clones or races.

Race: one or more clones which may be distinguished from other clones by pathogenic potential either quantitatively or qualitatively on a series of differential hosts.

Clones of *F. oxysporum* f. *cubense* will be designated by letters, cultivars by name, and in future studies races by arabic numerals.

Isolates that appeared consistently and in abundance from diseased tissue were transferred to 4-oz bottles containing peptone dextrose agar. These isolates are referred to as wild types in contrast to mutant types that appeared in culture and were not obtained from diseased bananas. Single microconidia cultures were obtained, and single spore stock cultures were maintained in tubes of sterile soil to prevent displacement of the wild type clones by cultural mutants (4). Comparison of clones was made on agar slants in 4-oz bottles or large test tubes (200×25 mm) maintained at a fluctuating air-conditioned room temperature of 22 to 27° C and exposed in racks to average diurnal diffuse room light.

Pathogenicity tests were undertaken by artificially inoculating healthy mature Gros Michel banana plants growing in two flood-fallowed areas. Soils were clay loam with a pH of 7.4 to 7.8 Areas to be utilized for pathogenicity studies were first surveyed several times over a period of 3 months. Only those sections or portions of sections free of Panama-diseased mats were chosen. It was established that during the experiments only a few scattered cases of natural infection appeared amounting to less than 1% of the mats in the experimental area. Plants 12 ft apart were inoculated by a trench being dug 4 to 6 in. deep for 3 ft around one side of a banana mat about 2 ft from the base of the mat (9). About 300 cc of a 2- to 3-week-old culture of *F. oxysporum* f. *cubense* grown on 10% corn meal-in-sand was sprinkled along the bottom and sides of the trench with care being taken to cover protruding banana root stubs. Disease symptoms began to appear within 6 to 10 weeks. Incidence of diseased mats, number of mats destroyed, and rate of spread to adjacent mats in the area were recorded for periods up to 12 months after inoculation. Check mats inoculated with corn meal-in-sand alone developed less than 1% disease, attributable to natural infection.

Results

Description of the Major Isolates and Syndromes Induced

Wild type isolates of *F. oxysporum* f. *cubense* fell into two clonal groups or cultivars designated 'Inodoratum' and 'Odoratum' (Table I) because of the presence or absence of a pronounced distinctive odor after 8 days on peptone dextrose agar. The odor was noticeable as early as 4 days after fungus transfer to peptone dextrose agar. A distinct but milder odor was also detected from 'Odoratum' clones growing on potato sucrose agar containing 2%

TABLE I

Distinguishing characteristics on various media after 8 days of the two major cultivars of *F. oxysporum* f. *cubense* isolated from diseased banana plants

Media	Cultivar	
	'Inodoratum'	'Odoratum'
Peptone dextrose agar with rose bengal and streptomycin, pH 6.4	No odor, mycelium white, compact, yellowish tinge to center of colony of some clones	Strong distinctive odor, mycelium white with purple cast and beginnings of zonation
Potato sucrose agar, pH 6.1	No or faint odor, mycelium white, usually compact, purple pigment present in center of colony and in agar with some clones	Mild distinctive odor, dirty greyish-white fluffy mycelium with zonation
Potato dextrose agar, pH 6.0	No odor, mycelium white, with purple pigment in center of colonies of some clones	Mild odor, dirty greyish-white fluffy mycelium with zonation
Steamed rice	No or faint odor, mycelium white with light-purple cast; varying amounts of purple pigment produced depending on clone	Very strong odor, mycelium white with strong pinkish cast tinged with purple

sucrose and agar and potato dextrose agar containing 1% dextrose and 2% agar after 8 to 12 days. No distinct odor was detectable from the 'Inodoratum' clones tested. The strongest odor was produced by the 'Odoratum' clones when growing on steamed rice for 8 days or longer. In addition to the difference between the two cultivars described in Table I, the 'Odoratum' cultivar produced 3 to 5 times more spores than the 'Inodoratum' on 10% corn meal-in-sand cultures and on peptone dextrose agar after growth for 3 to 7 days. On peptone dextrose agar the 'Inodoratum' cultivar grew radially about 12% faster than the 'Odoratum'.

The first aboveground symptom of Panama disease on Gros Michel bananas in the field is the appearance of a yellow streak or patch on the petiole of the oldest leaf or leaves. During the development of the disease from this initial symptom to death and collapse of all leaves from 3 to 6 weeks later, two syndromes became apparent in Honduras. In the yellowing syndrome (Fig. 1), there is a pronounced yellowing and necrosis of erect leaves. In the non-yellowing syndrome (Fig. 2), there is little or no yellowing of erect leaves but the leaves collapse as a result of buckling of the petiole and hang about the pseudostem as a green shroud for several days to a week before turning brown and dying. Cultures obtained from plants in certain areas showing pronounced leaf yellowing were predominately of the 'Inodoratum' cultivar. Cultures obtained from plants showing little or no leaf yellowing were predominately of the 'Odoratum' cultivar (Table II). Subsequent pathogenicity studies showed that inoculations with certain clones of the 'Inodoratum' cultivar such as clone C induced a strong yellowing syndrome in most plants whereas certain clones of the 'Odoratum' cultivar induced a non-yellowing syndrome in most plants.

TABLE II

Association between syndromes observed and cultivar of *Fusarium oxysporum* f. *cubense* isolated in Guaruma 2, flood fallow lake 1, Honduras

Syndrome in field	Per cent cultivar isolated*		
	'Inodoratum'	'Odoratum'	'Inodoratum' and 'Odoratum' mixed
Yellowing	50	32	18
Non-yellowing	0	100	0

*From a sampling of each of 150 plants exhibiting the yellowing (Fig. 1) and non-yellowing (Fig. 2) syndromes.

Occasionally as many as 10% of the colonies developing on peptone dextrose agar from blended diseased tissue were different from the major clones found within the two major cultivars listed in Table I. However, it did not appear that these miscellaneous clones existed in any quantity by themselves in

FIGS. 1 and 2. Yellowing (Fig. 1) and non-yellowing (Fig. 2) syndromes induced by certain clones of *F. oxysporum* f. *cubense* 'Inodoratum' and 'Odoratum', respectively, in Gros Michel bananas.

PLATE I

nature. Indeed, they may have been selected or favored as a result of culturing on the artificial substrate. Since their numbers did not indicate that they were important in determining disease behavior in the field they were not studied further at the time.

The following number of isolations were made from diseased Gros Michel banana plants from different areas: Honduras (various areas in the Ulua Valley), 350; Colombia (Rio Frio district), 50; British Cameroons, 3; Guatemala east coast, 15; Panama east coast, 10; Dominican Republic, 10. 'Inodoratum' and 'Odoratum' cultivars were obtained from Honduras, Dominican Republic, and Guatemala. The 'Odoratum' cultivar was obtained from the other areas. In general the 'Odoratum' cultivar was isolated 5 to 10 times more frequently than the 'Inodoratum' in Honduras. With the exception of Honduras and Colombia, there were not enough isolates from the other areas to determine cultivar distribution. It is noteworthy, however, that all isolates from Colombia were of the 'Odoratum' cultivar and no yellowing syndrome was observed in Colombia.

Cultural Interaction

It was observed on one set of plates containing blended tissue from a diseased plant that a raised white band of dense mycelium developed where certain clones of the 'Inodoratum' cultivar grew together (Fig. 3). Microscopic examinations showed that hyphal growth was stimulated in the zone of interaction and numerous swollen cells were present in the hyphae. This phenomenon was described by Miller (3) for *F. oxysporum* f. *niveum* and was designated cultural interaction.

Cultural interaction was used as a diagnostic tool in classifying and distinguishing clones of *F. oxysporum* f. *cubense*. Pairing a number of single spore isolates showed that clones of the 'Inodoratum' cultivar that appeared identical on peptone dextrose agar consisted of at least three clones (Table III). Two of these clones were designated cultural interactants I and II. When the clones comprising cultural interactants I and II were paired they reacted with a band of stimulated growth where the colonies joined. No reaction occurred when the identical clones were paired. Also, no members of the 'Odoratum' clonal group have reacted with cultural interaction.

Pathogenicity Studies

In banana wilt a single shoot within the cluster of three to four shoots that forms a mat may become diseased and die. The remaining shoots may stay healthy and continue to produce fruit for 1 to 3 years. The mat is said to have "recovered" from disease. Eventually, as disease intensity builds up in an area, disease recurs so frequently within a mat that the young shoots never mature or produce fruit and the mat eventually dies. This may take 2 years or longer. In general, the more rapid the appearance of disease and the destruction of the mat after planting the greater the disease intensity in a given area. Accordingly, differences in the pathogenicity of clones of *F. oxysporum* f. *cubense* were measured in the field using three criteria: (*a*)

TABLE III

Some distinguishing characteristics of various isolates of *Fusarium oxysporum* f. *cubense*

Cultivar	Predominant syndrome induced*	Clone	Reaction with cultural interactants†		Source	Relative pathogenicity‡
			I	II		
'Inodoratum'	Yellowing	A	+	−	Honduras	Moderately virulent
'Inodoratum'	Yellowing	B	−	−	Honduras	Very slightly virulent
'Inodoratum'	Yellowing	C	−	+	Honduras	Very highly virulent
'Odoratum'	Non-yellowing	D	−	−	Honduras	Moderately virulent
'Odoratum'	Non-yellowing	E	−	−	Panama	Highly virulent
'Odoratum'	Non-yellowing	F§	−	−	Colombia	Moderately virulent
'Odoratum'	Non-yellowing	G	−	−	British Cameroons	Slightly virulent

*See Figs. 1 and 2.
†Reaction when cultures paired in plates: + = cultural interaction occurred (Fig. 3); − = no cultural interaction.
‡See Tables IV and V, and Fig. 5.
§This clone appears different in colony appearance on potato sucrose agar from other 'Odoratum' clones.

TABLE IV

Effect on disease incidence of field inoculations of Gros Michel bananas growing in Mopala flood-fallowed lake with different clones of *F. oxysporum* f. *cubense* from Honduras

Plot No.	Mats per plot inoculated	Days after inoculated	Cultivar inoculated	Clone	No. of shoots diseased in mats inoculated*	No. of adjacent diseased mats	No. mats diseased in 85 mat square	No. mats inoculated not productive	Predominant syndrome induced
1	14	395	'Inodoratum'	C	32	18	36	6	Yellowing
2	14	395	'Odoratum'	D	6	8	18†	0	Non-yellowing†
3	9	313	'Inodoratum'	C	11	8	21	5	Yellowing
4	9	313	'Odoratum'	D	10	1	10†	0	Non-yellowing†

*Total number of newly diseased shoots in mats from all surveys.
†Cultural studies showed about 18 of these mats were infected with the 'Inodoratum' cultivar and some showed a leaf-yellowing syndrome.

rapidity of appearance of disease after inoculation; (*b*) rapidity of destruction of followers in the mat and the eventual destruction of the mat as a fruit-producing unit; (*c*) rapidity of disease spread to adjacent non-inoculated mats in the area.

Results of the first four pathogenicity experiments (Tables IV and V, Figs. 4 and 5) show that clone C (cultural interactant I) of the 'Inodoratum' cultivar from Honduras and clone E of the 'Odoratum' cultivar from Panama are much more virulent than the other clones. An additional two experiments were performed and confirmed the results of the first series of experiments.

TABLE V

Effect of inoculation with different clones of *F. oxysporum* f. *cubense* on incidence of Panama disease in Gros Michel bananas in Mopala and Omonita flood-fallowed lakes

Cultivar	Clone	Source	No. mats inoculated newly diseased			No. mats in two adjacent rows newly diseased			No. mats unproductive*
			Days after inoculation						
Experiment 1†			139	166	197	139	166	197	240
'Odoratum'	E	Panama	11	2	0	3	8	5	5
'Odoratum'	F	Colombia	2	2	1	2	3	3	0
'Odoratum'	D	Honduras	3	3	3	0	2	2	2
'Inodoratum'	B	Honduras	0	0	1	2	0	0	0
			Days after inoculation						
Experiment 2†			120	147	178	120	147	178	221
'Odoratum'	E	Panama	7	4	1	0	0	5	2
'Odoratum'	F	Colombia	1	2	0	0	0	4	0
'Odoratum'	D	Honduras	2	3	1	1	1	4	0
'Odoratum'	G	Br.Cameroons	0	1	1	0	0	0	0
'Inodoratum'	C	Honduras	13	1	1	11	10	11	36
'Inodoratum'	A	Honduras	1	3	2	1	2	2	0
'Inodoratum'	B	Honduras	0	0	0	0	0	0	0
			Days after inoculation						
Experiment 3			64	83	114	63	83	157	157
'Odoratum'	E	Panama	4	8	2	1	5	6	5
'Odoratum'	F	Colombia	1	2	8	0	3	1	4
'Odoratum'	D	Honduras	0	5	5	0	0	1	4
'Odoratum'	G	Br.Cameroons	0	2	0	0	4	1	0
'Inodoratum'	C	Honduras	10	3	2	0	3	2	12
'Inodoratum'	B	Honduras	0	0	0	0	0	0	0
			Days after inoculation						
Experiment 4			41	68	99	41	68	99	142
'Odoratum'	E	Panama	0	6	6	0	3	8	7
'Odoratum'	F	Colombia	0	2	4	0	2	1	0
'Odoratum'	D	Honduras	0	2	5	0	1	2	1
'Odoratum'	G	Br.Cameroons	0	0	2	0	0	0	0
'Inodoratum'	C	Honduras	0	5	9	0	1	9	14
'Inodoratum'	A	Honduras	0	1	4	0	2	2	0

*No. of mats in inoculated and two adjacent rows with destruction of progeny so great that no fruit is produced.
†Experiments 1 and 2 carried out in Mopala flood-fallowed lake, remaining experiments in Omonita flood-fallowed lake.

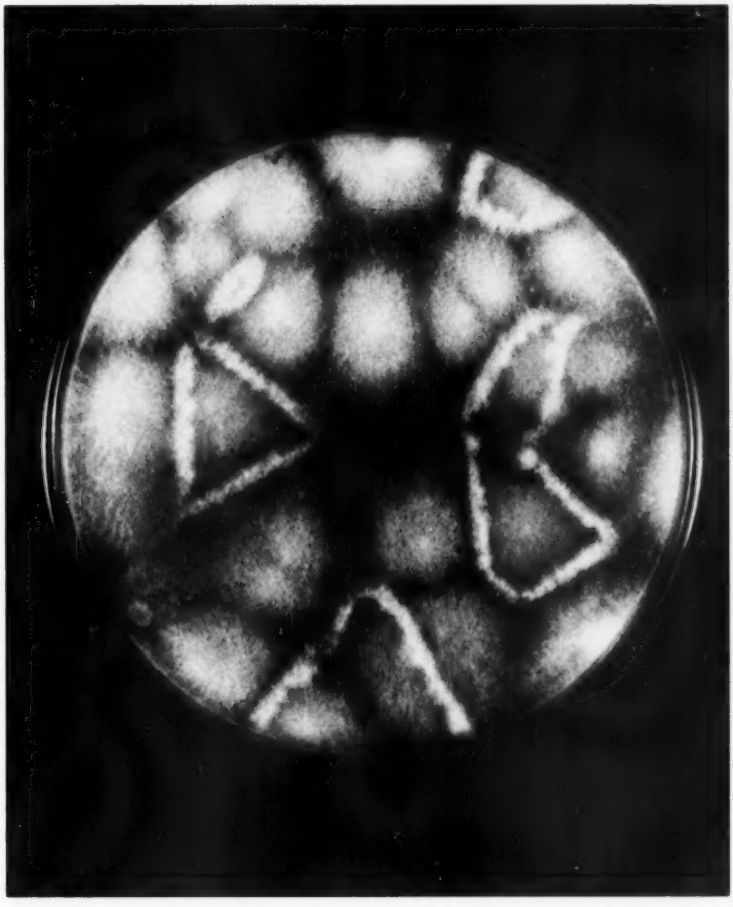

FIG. 3. Original plate of peptone dextrose agar containing blended diseased tissue from a dilution blank, from which cultural interactants I and II were isolated. Where colonies of interactants I and II joined, a zone of dense raised white mycelium developed. No interaction occurred when colonies of interactants I or II were paired with themselves.

FIG. 4. Aerial photo of bananas 221 days after being inoculated with clone C. Banana mats were being destroyed by disease. Adjacent areas inoculated with other clones showed little or no mat destruction even though many shoots were diseased.

As disease spread outward from plants inoculated with the 'Odoratum' cultivar in one experiment, some plants with a leaf-yellowing syndrome appeared and yielded an 'Inodoratum' clone (Table IV). This anomaly could be attributed to two factors: a mutation in the fungus derived from the original inoculum as it spread outward from the inoculated plants, or a rapid increase in disease originating from plants naturally infected with an 'Inodoratum' type clone within the experimental area. In all other cases, syndromes induced as a result of inoculation with these clones were predominately of the yellowing and non-yellowing types, respectively (Figs. 1 and 2). Clone C from Honduras and E from Panama, of which the former was the more virulent, induced more rapid appearance of disease, destruction of followers, and spread to adjacent mats than clones A, B, D, F, and G. The 'Odoratum'

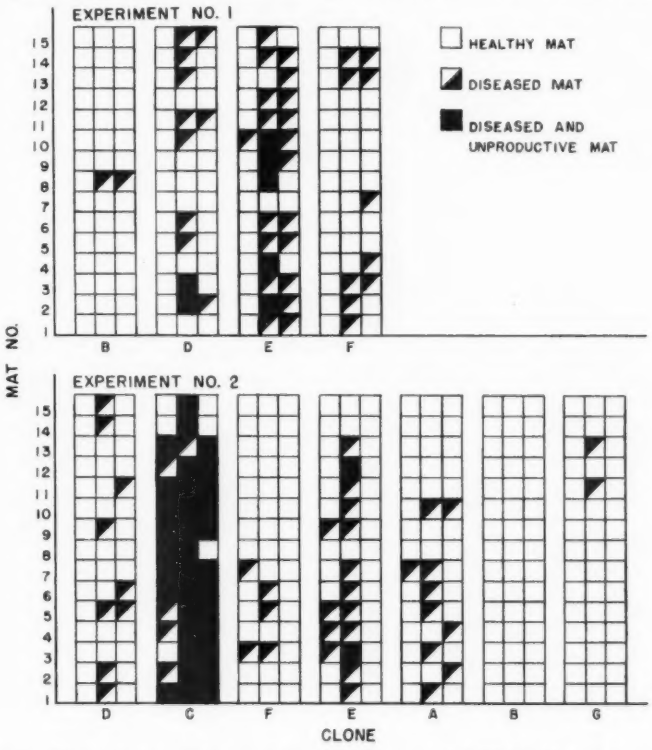

FIG. 5. Chart of plots of bananas in experiments 1 and 2 (Table V) inoculated with different clones of *F. oxysporum* f. *cubense* (only one adjacent row of non-inoculated mats on each side of the inoculated row is shown). Final disease readings were taken 197 days and 178 days after inoculation in experiments 1 and 2, respectively. The 15 numbered center mats were each inoculated with 300 cc of corn meal-in-sand culture. Experiment 1 clones are: B, Honduras 'Inodoratum'; D, Honduras 'Odoratum'; E, Panama 'Odoratum'; F, Colombia 'Odoratum'. Experiment 2 clones are: D, Honduras 'Odoratum'; C, Honduras 'Inodoratum'; F, Colombia 'Odoratum'; E, Panama 'Odoratum'; A, Honduras 'Inodoratum'; B, Honduras 'Inodoratum'; G, British Cameroons 'Odoratum'.

cultivar from Colombia was similar in pathogenicity to the clone D 'Odoratum' cultivar from Honduras. The clone of the 'Odoratum' cultivar from the British Cameroons appeared to be slightly less virulent than the Honduras and Colombia clones of the 'Odoratum' cultivar.

Discussion

Most isolates of *F. oxysporum* f. *cubense* from the rhizome or pseudostem of Gros Michel bananas can be designated as 'Inodoratum' or 'Odoratum' cultivars based on the absence or presence of pronounced distinctive odor on peptone dextrose agar and on other media including steamed rice. These findings are in agreement with Brandes (1), who recognized the presence or absence of odor as a convenient diagnostic tool in separating clones of *F. oxysporum* f. *cubense*. At least five morphologically or physiologically distinct clones of *F. oxysporum* f. *cubense* were present in certain diseased Gros Michel bananas containing the 'Inodoratum' and 'Odoratum' cultivars. These clones were distinguishable by morphological differences, cultural interaction, and pathogenicity. The three clones within the 'Inodoratum' cultivar were distinguishable from one another by cultural interaction and pathogenicity tests.

The 'Odoratum' cultivar appears to be more morphologically homogeneous in nature than the 'Inodoratum' cultivar but contains clones of differing degrees of virulence. In agar cultures many clones did not remain stable but produced various types of mutants. Further physiological tests in culture and pathogenicity studies will probably show that additional clones or races are present in the field in the 'Odoratum' cultivar. The 'Odoratum' cultivar is the most abundant in all areas and was found exclusive of 'Inodoratum' in Colombia. Even in Honduras, Dominican Republic, and Guatemala east coast, 'Inodoratum' was found much less frequently than 'Odoratum'.

The existence of clones of *F. oxysporum* f. *cubense* differing in pathogenicity is reported for the first time in this paper. It has been frequently observed that individual shoots within a banana mat become diseased intermittently over a period of several years. Nevertheless, healthy shoots that produce fruit frequently follow the diseased shoots. The frequency of fruit production by a diseased mat may be partly influenced by the virulence of the clone of *Fusarium* attacking the mat. As the inoculum potential builds up over a period of several years, however, all mats are eventually destroyed by the disease. The process could be delayed for a few months to a few years where less virulent clones are involved. A group of different *Musa* spp. hosts is now being propagated for further pathogenicity studies and for classification of clones into races based on the disease response of these differential hosts.

These studies show that a system of clonal grouping into cultivars is necessary in describing wild type isolates of *F. oxysporum* f. *cubense*. A cultivar that appears identical morphologically may, by various physiological tests using single microconidial cultures, yield several clones. The number of clones occurring in abundance in nature, however, appear far fewer than those developing in cultures. Many of the clones, particularly of the 'Inodoratum'

cultivar, did not remain stable in culture unless maintained in soil. The occasional appearance of a few colonies of a non-classifiable type among colonies of the classifiable clonal groups or cultivars suggests that mutants are present in nature. However, their paucity in numbers suggests that they may have slight survival value or have not increased in competition with the major cultivars.

The association in Honduras between the leaf-yellowing syndrome and the 'Inodoratum' cultivar and the non-leaf-yellowing syndrome and the 'Odoratum' cultivar indicates that the physiology of host–parasite relationship is different between cultivars. Apparently physiological responses between host and parasite clone that induce yellowing of erect leaves or leaf petiole collapse with little or no yellowing are distinctive. It is noteworthy, however, that in naturally infected plants in the field not all plants exhibiting yellowing of erect leaves yield 'Inodoratum' clones. Thus other factors perhaps environmental are also involved in syndrome development. Ward (12) distinguished two syndromes in Malaya which he designated chronic and acute forms of banana wilt. Also, Prendergast (5) distinguishes a chronic from an acute form of *Fusarium* wilt of oil palm. The former is characterized by drying and collapse of leaf petioles and the latter by death of erect fronds which later collapse.

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THE OCCURRENCE OF FUSARIUM SPECIES IN CANADA

VI. TAXONOMY AND GEOGRAPHIC DISTRIBUTION OF FUSARIUM SPECIES ON PLANTS, INSECTS, AND FUNGI[1]

W. L. GORDON[2]

Abstract

The present investigation was commenced in 1932 and has been continued annually since that time with the object of determining the identity, host range, and geographic distribution of the *Fusarium* species in Canada. Approximately 9000 isolates of *Fusarium* were studied. These isolates were obtained from 173 species and botanical varieties of plants, 14 species of insects, and 4 of fungi. Of the various species and botanical varieties of plants from which isolates were obtained, 19 were cereals and grasses, 19 were vegetable crops, 15 were fruit crops, 13 were field crops, 52 were ornamental plants, 31 were trees and shrubs, and 24 were common weed plants. Less than 1% of the total isolates was obtained from insects and fungi. Although most of the isolates originated in Manitoba, some were obtained from each of the other provinces of Canada except Newfoundland.

A total of 18 species, 3 varieties, and 18 formae of *Fusarium*, classified in nine sections of the genus, were identified among the isolates from plants, insects, and fungi. These species, varieties, and formae are: *F. chlamydosporum* Wr. & Rg., *F. poae* (Pk.) Wr., *F. sporotrichioides* Sherb. (section Sporotrichiella); F. *arthrosporioides* Sherb., *F. avenaceum* (Fr.) Sacc. (Roseum); *F. concolor* Rg., *F. semitectum* Berk. & Rav. (Arthrosporiella); *F. acuminatum* (Ell. & Ev.) Wr., *F. equiseti* (Cda.) Sacc. (Gibbosum); *F. culmorum* (W. G. Sm.) Sacc., *F. graminearum* Schwabe, *F. heterosporum* Nees emend. Raillo, *F. sambucinum* Fuckel, *F. samb.* var. *coeruleum* Wr., *F. samb.* f. 6 Wr. (Discolor); *F. moniliforme* Sheld., *F. moniliforme* var. *subglutinans* Wr. & Rg. (Liseola); *F. lateritium* Nees (Lateritium); *F. oxysporum* Schl. emend. S. & H., *F. oxysporum* var. *redolens* (Wr.) Gordon, *F. oxysporum* f. *betae* (Stewart) S. & H., f. *callistephi* (Beach) S. & H., f. *cepae* (Hanz.) S. & H., f. *conglutinans* (Wr.) S. & H., f. *dianthi* (Prill. & Del.) S. & H., f. *fabae* Yu & Fang, f. *gladioli* (Massey) S. & H., f. *lilii* Imle, f. *lini* (Bolley) S. & H., f. *lycopersici* (Sacc.) S. & H., f. *melonis* S. & H., f. *narcissi* S. & H., f. *pini* (Hartig) S. & H., f. *tuberosi* S. & H. (Elegans); *F. solani* (Mart.) App. & Wr. emend. S. & H., *F. solani* f. *eumartii* (Carp.) S. & H., f. *phaseoli* (Burk.) S. & H., f. *pisi* (Jones) S. & H., *F. coeruleum* (Lib.) Sacc. (Martiella).

F. chlamydosporum, *F. heterosporum*, *F. moniliforme* var. *subglutinans*, as well as 14 formae of *F. oxysporum* and 3 formae of *F. solani*, are reported to occur in Canada for the first time in this series of papers.

The six species isolated most commonly, as indicated by the number of hosts from which they were obtained, are *F. oxysporum*, *F. acuminatum*, *F. solani*, *F. equiseti*, *F. avenaceum*, and *F. poae*.

The conidia and chlamydospores of *F. chlamydosporum* and *F. heterosporum* are illustrated by drawings.

Introduction

The writer started in 1932 to investigate the occurrence of *Fusarium* species in Canada. Since that time he has isolated them from various habitats. Previous papers in this series have dealt with their identity and occurrence in two important habitats, namely, agricultural seeds (2, 3, 4) and agricultural soils (5, 6). The present paper is concerned primarily with the taxonomy and geographic distribution of those species, varieties, and forms of *Fusarium* that have been isolated, during the investigations carried on annually since 1932, from cultivated and other plants, from insects, and from fungi.

[1]Manuscript received November 10, 1958.
Contribution No. 13 from Canada Department of Agriculture Research Laboratory, Winnipeg, Manitoba.
[2]Plant Pathology Section.

Materials and Methods

Approximately 9000 isolates of *Fusarium* were studied in the present investigation. Most of the isolates from plants were obtained during investigations of the etiology of some diseased condition such as foot rot, wilt, canker, dieback, blight, discolorations, decays, and the like. A few isolates were obtained from apparently healthy plants.

Except when isolates could be obtained directly from conidia or other fruiting bodies on the surface of the host, isolates were made following surface disinfection of tissues. A mixture of mercuric chloride and alcohol was usually employed as the surface disinfectant. This treatment was followed by one or more rinses in sterile water before pieces of the host tissue were plated out on potato sucrose agar (2% sucrose, 2% agar) with or without acidification.

Isolates were obtained from a total of 173 species and botanical varieties of plants, 14 species of insects, and 4 of fungi. Of the various species and varieties of plants which yielded isolates of *Fusarium*, 19 were cereals and grasses, 19 were vegetable crops, 15 were fruit crops, 13 were field crops, 52 were ornamental plants, 31 were trees and shrubs, and 24 were common weed plants. Less than 1% of the total isolates was obtained from insects and fungi.

Although most of the isolates originated in Manitoba, some were received from eight other provinces, namely, British Columbia, Alberta, Saskatchewan, Ontario, Quebec, New Brunswick, Nova Scotia, and Prince Edward Island.

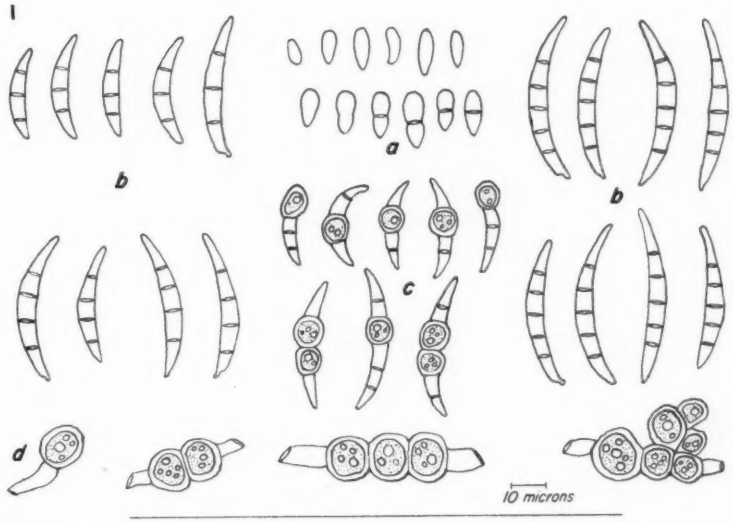
Drawings of conidia and chlamydospores were made with the aid of a camera lucida at a microscope magnification of approximately 700×.

In the data presented in the taxonomic section of this paper about the origin of isolates, the date denotes when the writer obtained the first isolate of a species, variety, or form of *Fusarium* from a particular host and province.

Taxonomy of the Isolates of *Fusarium*

The system of nomenclature and taxonomy followed in naming and classifying the wild type isolates of *Fusarium* obtained during this investigation is essentially the same as that described and employed in Part II of this series of papers (3). The system is basically that of Wollenweber and Reinking (13), modified where it appeared to be desirable according to recent revisions of the genus by Snyder and Hansen (8, 9, 10), Raillo (7), and Bilai (1). According to the system of nomenclature and classification adopted by the writer, a total of 18 species, 3 varieties, and 18 formae of *Fusarium* were distinguished and identified among the isolates from plants, insects, and fungi during this investigation. These species, varieties, and formae represented nine sections of the genus, namely, Sporotrichiella, Roseum, Arthrosporiella, Gibbosum, Discolor, Lateritium, Liseola, Elegans, and Martiella.

The synonymy of the species, varieties, and forms of *Fusarium* given in this paper is by no means complete but includes those names that are most frequently encountered in the literature of *Fusarium* at the present time.



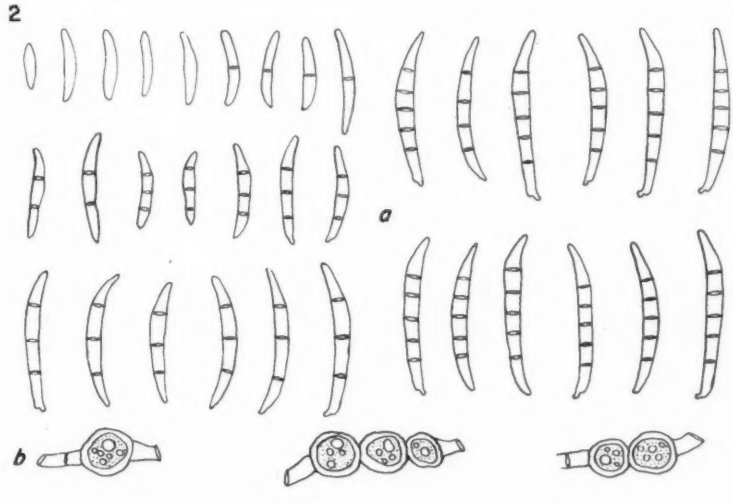


FIG. 1. *F. chlamydosporum* (section Sporotrichiella). *a*, microconidia; *b*, macroconidia; *c*, chlamydospores in macroconidia; *d*, chlamydospores in mycelium.
FIG. 2. *F. heterosporum* (section Discolor). *a*, conidia; *b*, chlamydospores in mycelium.

A more extensive synonymy is given by Wollenweber (11, 12), Wollenweber and Reinking (13), Snyder and Hansen (8, 9, 10), Raillo (7), Bilai (1), and by the writer in previous papers (3, 4, 6).

Section Sporotrichiella Wr.

Wollenweber and Reinking, Die Fusarien, pp. 45–47. 1935.
Raillo, Fungi of the genus *Fusarium*, pp. 192–194. 1950.
Bilai, The Fusaria, pp. 274–276. 1955.

Three species, namely *F. chlamydosporum* Wr. & Rg., *F. poae* (Pk). Wr., and *F. sporotrichioides* Sherb., classified in this section of the genus, have been isolated from plants in Canada. Only *F. poae* was isolated from insects and fungi.

Fusarium chlamydosporum Wr. & Rg. (Fig. 1)

Wollenweber and Reinking, Die Fusarien, pp. 47–48. 1935.
Syn. *F. tricinctum* (Cda.) Sacc. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.
F. sporotrichioides Sherb. emend. Raillo pr. p.
Raillo, Fungi of the genus *Fusarium*, p. 196. 1950.
F. sporotrichiella Bilai var. *sporotrichioides* (Sherb.) Bilai pr. p.
Bilai, The Fusaria, pp. 277–278. 1955.

PLANTS

Triticum durum Desf. (durum wheat). Isolated from blighted heads of Dakar wheat in the International Rust Nursery. Man., 1957.

Fusarium poae (Pk.) Wr.

Wollenweber and Reinking, Die Fusarien, p. 47. 1935.
Raillo, Fungi of the genus *Fusarium*, pp. 194–195. 1950.
Bilai, The Fusaria, p. 277. 1955.
Syn. *F. tricinctum* (Cda.) Sacc. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.
F. tricinctum (Cda.) Sacc. emend. Snyder & Hansen f. *poae* Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.
F. poae (Pk.) Wr. form 1 Raillo
Raillo, Fungi of the genus *Fusarium*, p. 195. 1950.
F. sporotrichiella Bilai pr. p.
Bilai, The Fusaria, pp. 276–277. 1955.
F. sporotrichiella Bilai var. *poae* (Pk.) Bilai
Bilai, The Fusaria, p. 277. 1955.

PLANTS

Agropyron pauciflorum (Schwein.) Hitchc. (slender wheat grass). Isolated from the basal parts of blighted seedlings. Sask., 1937.
Allium cepa L. (onion). Isolated from purple blotched areas of seed stalks. Man., 1936.
Avena sativa L. (oat). Isolated from diseased basal parts of adult plants, Man., 1932; from blighted spikelets, N.B., N.S., and P.E.I., 1938; from conidia produced abundantly on the leaves, Man., 1956.
Bromus inermis Leyss. (brome grass). Isolated from diseased basal parts of adult plants. Man., 1933.
Cucumis sativus L. (cucumber). Isolated from diseased basal parts. Man., 1933.
Cucurbita maxima Duchesne (squash). Isolated from decayed areas on the surface of fruit displayed on the Winnipeg market. Man., 1936.
Festuca rubra L. (red fescue). Isolated from the heads and sheaths of creeping red fescue. Alta., 1953.
Fragaria chiloensis Duchesne var. *ananassa* Bailey (cultivated strawberry). Isolated from diseased roots. N.S., 1940.

Gladiolus sp. (gladiolus). Isolated from bulbels with a soft, basal rot. Man., 1937.
Hordeum vulgare L. (barley). Isolated from diseased basal parts of adult plants, Man., 1932; B.C., 1938; from blighted heads, N.B. and N.S., 1937; B.C. and P.E.I., 1938; Que., 1944; Ont., 1948; Man., 1949.
Linum usitatissimum L. (flax). Isolated from basal parts. Sask., 1948.
Malus sylvestris Mill. (apple). Isolated from a limb canker. N.S., 1939.
Medicago sativa L. (alfalfa). Isolated from diseased basal parts. Man., 1934; Alta., 1935.
Melilotus alba Desr. (white sweet clover). Isolated from diseased basal parts. Man., 1934.
Paeonia lactiflora Pall. Isolated from blighted stems along with *Botrytis paeoniae* Oudem. Man., 1935.
Pinus resinosa Ait. (red pine). Isolated from damped-off seedlings. Ont., 1949.
Rubus idaeus L. (red raspberry). Isolated from wilted plants, Que., 1934; from plants with dieback, Ont., 1936.
Salix sp. (willow). Isolated from twigs. Que., 1952.
Sambucus racemosa L. (European red elder). Isolated from branches with dieback. Sask., 1955.
Secale cereale L. (rye). Isolated from blighted heads. Man., 1935.
Trifolium pratense L. (red clover). Isolated from discolored tissue of stems and roots. Ont., 1951; Que., 1954.
Triticum aestivum L. (common wheat). Isolated from diseased basal parts of adult plants, Man., 1932; from blighted heads, Man., 1932; Ont., 1935; Que., N.B., N.S., and P.E.I., 1938; B.C., 1940; Alta., 1941; Sask., 1942; from conidia produced abundantly on the nodes and leaves of Kubanka wheat, Man., 1939.
Triticum dicoccum Schrank. (emmer). Isolated from blighted heads. P.E.I., 1940; Que., 1941; Man., 1942.
Triticum durum Desf. (durum wheat). Isolated from blighted heads. Man., 1937.
Tulipa gesneriana L. (common tulip). Isolated from decayed roots along with *Cylindrocarpon radicicola* Wr. Man., 1939.
Ulmus americana L. (American elm). Isolated from twigs with dieback. Man., 1939.
Zea mays L. (corn). Isolated from blighted seedlings, Man., 1936; from rotted cobs, Man., 1942; from conidial masses on overwintered corn stalks in contact with soil, Man., 1949.

INSECTS

Carpocapsa pomonella (L.) (codling moth). Isolated from larvae. N.S., 1949.
Melanoplus bivittatus (Say) (two-striped grasshopper). Isolated from dead insects. Man., 1939.
Musca domestica L. (housefly). Isolated from dead flies adhering to windowpanes. Man., 1934.
Paraclemensia acerifoliella (Fitch) (maple leaf cutter). Ont., 1949.
Pristiphora erichsonii (Htg.) (larch sawfly). Ont., 1949.

FUNGI

Ustilago hordei (Pers.) Lagerh. (covered smut of barley). Isolated from mycelium on a smutted inflorescence. Man., 1938.
Ustilago kolleri Wille (covered smut of oats). Isolated from mycelium on a smutted inflorescence. Man., 1942.

FUSARIUM SPOROTRICHIOIDES Sherb.

Wollenweber and Reinking, Die Fusarien, pp. 48–49. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 196. 1950.
Bilai, The Fusaria, 277–278. 1955.
Syn. *F. tricinctum* (Cda.) Sacc. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.
F. tricinctum (Cda.) Sacc. emend. Snyder & Hansen f. *poae* (Pk.) Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, p. 663. 1945.
F. sporotrichiella Bilai pr. p.
Bilai, The Fusaria, pp. 276–277. 1955.
F. sporotrichiella Bilai var. *sporotrichioides* (Sherb.) Bilai
Bilai, The Fusaria, pp. 277–278. 1955.

PLANTS

Acer negundo L. (box elder). Isolated from discolored twigs. Man., 1932.
Agropyron pauciflorum (Schwein.) Hitchc. (slender wheat grass). Isolated from basal parts of blighted seedlings. Sask., 1937.
Avena sativa L. (oat). Isolated from the diseased basal parts of plants exhibiting premature blight. Man., 1946.
Hordeum vulgare L. (barley). Isolated from blighted heads. Sask., 1946.
Lathyrus venosus Muhl. (veiny sweet pea). Isolated from discolored areas on the stems. Man., 1949.
Pinus banksiana Lamb. (jack pine). Isolated from sporodochia on a branch. Ont., 1940.
Populus tremuloides Michx. (American aspen). Isolated from dead branches. Man., 1933.
Rubus idaeus L. (red raspberry). Isolated from wilted canes. Que., 1932.
Sambucus racemosa L. (European red elder). Isolated from decayed stem bases. Sask., 1945.
Solanum tuberosum L. (potato). Isolated from decayed tubers. Man., 1944.
Triticum aestivum L. (common wheat). Isolated from plants with foot rot, Man., 1933; Ont., 1941; from sterile spikelets, Que., 1937; from snow mold of winter wheat, B.C., 1951.
Triticum durum Desf. (durum wheat). Isolated from plants with foot rot, Man., 1933; from blighted heads, Man., 1942.
Ulmus americana L. (American elm). Isolated from chips from discolored twigs. Que., 1948.

Section Roseum Wr.

Wollenweber and Reinking, Die Fusarien, pp. 49–53. 1935.
Raillo, Fungi of the genus *Fusarium*, pp. 181–185. 1950.
Syn. Section Roseum Wr. emend. Bilai pr. p.
Bilai, The Fusaria, pp. 255–257. 1955.

Two species, namely *F. arthrosporioides* Sherb. and *F. avenaceum* (Fr.) Sacc., classified in this section, were isolated from plants and insects. *F. avenaceum* only was isolated from fungi.

Fusarium arthrosporioides Sherb.

Wollenweber and Reinking, Die Fusarien, pp. 56–57. 1935.
Syn. *F. roseum* Lk. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.

PLANTS

Avena sativa L. (oat). Isolated from plants with foot rot. Man., 1942.
Prunus persica Batsch (peach). Isolated from rotted fruit. Man., 1932.
Trifolium repens L. (white clover). Isolated from lesions on the stolons of Ladino clover. Ont., 1951.

INSECTS

Actebia fennica Tausch. (black army cutworm). Ont., 1949.

Fusarium avenaceum (Fr.) Sacc.

Wollenweber and Reinking, Die Fusarien, pp. 53–55. 1935.
Raillo, Fungi of the genus *Fusarium*, pp. 185–187. 1950.
Bilai, The Fusaria, pp. 257–258. 1955.
Syn. *F. roseum* Lk. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.
F. avenaceum (Fr.) Sacc. ssp. *volutum* (Wr.) Raillo
Raillo, Fungi of the genus *Fusarium*, pp. 188–189. 1950.
F. avenaceum (Fr.) Sacc. ssp. *volutum* Wr. var. *triseptatum* Raillo
Raillo, Fungi of the genus *Fusarium*, p. 189. 1950.

PLANTS

Allium cepa L. (onion). Isolated from decayed bulbs along with *F. oxysporum* Schl. f. *cepae* (Hanz.) Snyder & Hansen, Man., 1935; with *Botrytis allii* Munn., Ont., 1949.
Avena sativa L. (oat). Isolated from plants with foot rot, Man., 1932; Ont. and B.C., 1934; from blighted spikelets, N.S., 1938; N.B., 1955; from discolored nodes and stems, Que., 1948.

Brassica oleracea L. var. *capitata* L. (cabbage). Isolated from basal parts of plants with yellows along with *F. oxysporum* f. *conglutinans* (Wr.) Snyder and Hansen. Que., 1952.
Caragana arborescens Lam. (caragana). Isolated from discolored basal parts of wilted plants along with *Fusarium solani* (Mart.) App. & Wr. emend. Snyder & Hansen. Man., 1934.
Dahlia pinnata Cav. (dahlia). Isolated from decayed buds. Man., 1934.
Daphne mezereum L. Isolated from sporodochia on cankered branches. Ont., 1937.
Daucus carota L. var. *sativa* DC. (carrot). Isolated from decayed roots in storage. Ont., 1949.
Dianthus caryophyllus L. (carnation). Isolated from diseased stems. N.S., 1951.
Fragaria chiloensis Duchesne var. *ananassa* Bailey (cultivated strawberry). Isolated from diseased roots. N.S., 1940.
Hordeum vulgare L. (barley). Isolated from plants with foot rot, Man., 1932; from blighted heads, N.S. and N.B., 1937; Que., 1949.
Juglans cinerea L. (butternut). Isolated from discolored lesions on the fruit. Man., 1944.
Linum usitatissimum L. (flax). Isolated from basal parts of wilted plants. B.C., 1944; Man., 1948; Que., 1949.
Malus sylvestris Mill. (apple). Isolated from decayed fruit. Man., 1942.
Matthiola incana R. Br. (stock). Isolated from basal parts of plants with foot rot and wilt. Ont., 1936.
Medicago sativa L. (alfalfa). Isolated from basal parts of plants with foot rot. Man., Sask., Alta., 1935; Ont., 1952.
Melilotus alba Desr. (white sweet clover). Isolated from lesions on basal parts of stem. Man., 1934; Ont., 1945.
Penstemon procerus Dougl. Isolated from a leaf spot. Man., 1944.
Phleum pratense L. (timothy). Isolated from decayed culms. Que., 1940.
Pinus resinosa Ait. (red pine). Isolated from damped-off seedlings. Ont., 1948.
Pisum sativum L. (pea). Isolated from plants with foot rot. Man., 1949; Ont., 1955.
Rubus idaeus L. (red raspberry). Isolated from diseased raspberry canes. Ont., 1943.
Rubus occidentalis L. (blackcap raspberry). Isolated from lesions on canes. N.S., 1945.
Sambucus racemosa L. (European red elder). Isolated from discolored stem bases. Sask., 1945.
Secale cereale L. (rye). Isolated from plants with foot rot, Man., 1932; from blighted heads of winter rye, N.B., 1937.
Solanum tuberosum L. (potato). Isolated from decayed potato tubers in storage. Ont., 1937; P.E.I., 1952.
Trifolium pratense L. (red clover). Isolated commonly from decayed roots, Que., 1940; from discolored stem tissues, Ont., 1952.
Trifolium repens L. (white clover). Isolated from lesions on Ladino stolons. Ont., 1951.
Triticum aestivum L. (common wheat). Isolated from plants with foot rot, Man., 1933; Sask., 1936; from blighted heads, Man., 1935; B.C., N.B., Que., 1937; N.S. and P.E.I., 1938; Ont., 1941.
Triticum durum Desf. (durum wheat). Isolated from diseased basal parts, Man., 1932; from blighted heads, N.S., 1951; Que., 1955.
Tsuga canadensis Carr. (Canada hemlock). Isolated from discolored wood. B.C., 1951.
Zea mays L. (corn). Isolated from blighted seedlings. Man., 1936.

INSECTS

Choristoneura fumiferana (Clem.) (spruce budworm). Ont., 1949.
Hypera punctata (F.) (clover-leaf weevil). Man., 1948.

FUNGI

Melampsora lini (Pers.) Lev. (flax rust). Isolated from discolored rust pustules. Man., 1949; Ont., 1951.

Section Arthrosporiella Sherb.

Wollenweber and Reinking, Die Fusarien, pp. 57–58. 1935.
Raillo, Fungi of the genus *Fusarium*, pp. 162–165. 1950.
Gordon, Can. J. Botany, 30: 222. 1952.
Syn. Section Roseum Wr. emend. Bilai pr. p.
Bilai, The Fusaria, pp. 255–257. 1955.

F. concolor Rg. and *F. semitectum* Berk. & Rav., belonging in this section of the genus, were isolated infrequently from plants and not at all from insects and fungi.

FUSARIUM CONCOLOR Rg.

Wollenweber and Reinking, Die Fusarien, p. 60. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 164. 1952.
Syn. *F. roseum* Lk. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.
F. semitectum Berk. & Rav. var. *majus* Wr. emend. Bilai pr. p.
Bilai, The Fusaria, p. 259. 1955.

PLANTS

Gladiolus sp. (gladiolus). Isolated from bulbels with a wet, basal rot. Man., 1937.
Symphoricarpos occidentalis Hook. (wolfberry). Isolated from the decayed stem base of a seedling growing in the greenhouse. Man., 1938.

FUSARIUM SEMITECTUM Berk. & Rav.

Wollenweber and Reinking, Die Fusarien, pp. 58–59. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 163. 1950.
Bilai, The Fusaria, pp. 258–259. 1955.
Syn. *F. roseum* Lk. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.
F. semitectum Berk. & Rav. form 1 Raillo
Raillo, Fungi of the genus *Fusarium*, p. 163. 1950.

PLANTS

Agropyron smithii Rydb. (blue couch grass). Isolated from discolored areas on the basal leaves of this grass growing in a patch. Man., 1945.
Betula papyrifera Marsh. (paper birch). Isolated from brown stained wood taken from a tree trunk. Ont., 1953.
Cucumis melo L. var. *cantalupensis* Naud. (cantaloupe). Isolated from the basal parts of a wilted plant. Man., 1938.
Glycine max Merr. (soybean). Isolated from a leaf spot. Man., 1943.
Ulmus americana L. (American elm). Isolated from twigs with dieback. Man., 1939.

Section Gibbosum Wr.

Wollenweber and Reinking, Die Fusarien, pp. 61–62. 1935.
Raillo, Fungi of the genus *Fusarium*, pp. 165–170. 1950.
Gordon, Can. J. Botany, 30: 223–224. 1952.
Syn. Section Discolor Wr. emend. Bilai pr. p.
Bilai, The Fusaria, p. 259. 1955.

Two species, namely *F. acuminatum* (Ell. & Ev.) Wr. and *F. equiseti*, classified in this section of the genus, were isolated commonly from plants. Both species were also isolated from insects but not from fungi.

FUSARIUM ACUMINATUM (Ell. & Ev.) Wr.

Wollenweber, J. Agr. Research, 2: 269–270. 1914.
Raillo, Fungi of the genus *Fusarium*, pp. 177–178. 1950.
Gordon, Can. J. Botany, 30: 226. 1952.
Syn. *F. scirpi* (Lamb. & Fautr.) var. *acuminatum* (Ell. & Ev.) Wr.
Wollenweber and Reinking, Die Fusarien, p. 67. 1935.
F. gibbosum App. & Wr. emend. Bilai var. *acuminatum* (Ell. & Ev.) Bilai pr. p.
Bilai, The Fusaria, p. 263. 1955.
F. roseum Lk. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.

F. roseum Lk. emend. Snyder & Hansen, f. *cerealis* (Cke.) Snyder & Hansen pr. p. Snyder and Hansen, Am. J. Botany, 32: 663–664. 1945.

PLANTS

Acer negundo L. (box elder). Isolated from overwintered seed. Man., 1946.

Agropyron cristatum (L.) Beauv. (crested wheat grass). Isolated from diseased basal parts. Sask., 1937.

Agropyron pauciflorum (Schwein.) Hitchc. (slender wheat grass). Isolated from diseased parts. Sask., 1937.

Allium cepa L. (onion). Isolated from bulbs with basal rot along with *Fusarium oxysporum* Schl. f. *cepae.* (Hanz.) Snyder & Hansen, Man., 1941; from a wilted seedling of the variety White Portugal, B.C., 1943.

Antirrhinum majus L. (snapdragon). Isolated from basal parts of wilted plants, Man., 1937; from damped-off seedlings growing in a greenhouse, Man., 1938.

Asclepias syriaca L. (silky milkweed). Isolated from discolored basal parts. Man., 1938.

Avena sativa L. (oat). Isolated from diseased basal parts. Man., 1933.

Betula lutea Michx. (yellow birch). Isolated from discolored wood. Ont., 1951.

Brassica napobrassica Mill. (swede). Isolated from decayed tap roots. Man., 1945.

Bromus inermis Leyss. (brome grass). Isolated from diseased parts. Man., 1932.

Callistephus chinensis Nees (China aster). Isolated from basal parts of wilted plants along with *Fusarium oxysporum* Schl. f. *callistephi* (Beach) Snyder & Hansen. Man., 1939.

Canna generalis Bailey (canna). Isolated from decayed roots. Man., 1944.

Caragana arborescens Lam. (caragana). Isolated from discolored basal parts of wilted plants along with *Fusarium solani* (Mart.) App. & Wr. emend. Snyder & Hansen, Man., 1938; Sask., 1949; from chlorotic seedlings, Sask., 1953.

Carthamus tinctorius L. (safflower). Isolated from plants with foot rot. Man., 1956.

Chenopodium album L. (lamb's-quarters). Isolated from basal parts of apparently healthy plants. Man., 1938.

Chrysanthemum sp. Isolated from plants with foot rot along with *Fusarium solani* (Mart.) App. & Wr. emend. Snyder & Hansen. Man., 1938.

Cirsium arvense (L.) Scop. (Canada thistle). Isolated from decayed basal parts. Man., 1944.

Citrullus vulgaris Schrad. (watermelon). Isolated from decayed fruit, Man., 1938; from basal parts of plants with foot rot, Man., 1940.

Cleome spinosa L. (giant spiderflower). Isolated from diseased basal parts of wilted plants. Man., 1954.

Cucumis melo L. var. *cantalupensis* Naud. (cantaloupe). Isolated from the basal parts of wilted plants. Man., 1935.

Cucumis sativus L. (cucumber). Isolated from decayed green fruit, Man., 1938; from the basal parts of wilted plants, Man., 1940.

Cucurbita maxima Duchesne (squash). Isolated from decayed areas in a fruit obtained from the Winnipeg market. Man., 1936.

Daucus carota L. var. *sativa* DC. (carrot). Isolated from the tap root of carrots affected by aster yellows, Man., 1938; from decayed Imperator carrots in storage, B.C., 1943.

Dianthus chinensis L. (rainbow pink). Isolated from diseased basal parts of wilted plants. Man., 1939.

Dracocephalum parviflorum Nutt. (false dragonhead). Isolated from the basal parts of apparently healthy plants. Man., 1938.

Elaeagnus angustifolia L. (Russian olive). Isolated from diseased basal parts of plants. Sask., 1943.

Erysimum cheiranthoides L. (wormseed mustard). Isolated from basal parts of plants. Man., 1938.

Euonymus alatus Sieb. Isolated from branches with dieback along with *Fusarium lateritium* Nees. B.C., 1940.

Euphorbia esula L. (leafy spurge). Isolated from basal parts of plants. Man., 1938.

Fragaria chiloensis Duchesne var. *ananassa* Bailey (cultivated strawberry). Isolated from diseased roots along with *Cylindrocarpon radicicola* Wr. Man., 1938.

Galium boreale L. (northern bedstraw). Isolated from discolored roots. Man., 1938.

Gladiolus sp. (gladiolus). Isolated from corms with a reddish-colored decay. Isolate shown to be pathogenic to corms after wounding. Man., 1939.

Glycine max Merr. (soybean). Isolated from lesions on the base of stem and on the roots. Man., 1943.

Helianthus annuus L. (sunflower). Isolated from basal parts of wilted plants along with *Pythium* sp., Sask., 1943; from a foot rot of plants growing in the field, Man., 1946; from seedlings growing in the greenhouse, Man., 1953.

Hordeum vulgare L. (barley). Isolated from diseased basal parts of adult plants, Man., 1932; from blighted heads of barley, Sask., 1946; Que., 1949; Man., 1956; from badly discolored seed, Alta., 1943.

Impatiens balsamina L. (garden balsam). Isolated from the basal parts of plants with foot rot. Man., 1941.

Linum usitatissimum L. (flax). Isolated from roots and other basal parts of wilted plants, Man., 1937; from blighted seedlings along with *Rhizoctonia solani* Kühn, Man., 1938; Sask., 1948; from stem canker lesions, Man., 1948.

Lupinus hirsutus L. (blue lupine). Isolated from the basal parts of plants with foot rot. Man., 1937.

Lupinus polyphyllus Lindl. (lupine). Isolated from lesions on the cotyledons of seedlings growing in a greenhouse. Man., 1938.

Lycopersicum esculentum Mill. (tomato). Isolated from decayed fruit. Man., 1943. This isolate was pathogenic through wounds, to green fruit in laboratory tests.

Malus baccata Borkh. (Siberian crab apple). Isolated from basal parts of winter-injured seedlings. Man., 1951.

Malus sylvestris Mill. (apple). Isolated from discolored roots of winter-injured plants. Man., 1951.

Medicago sativa L. (alfalfa). Isolated from diseased basal parts of plants, Alta., 1935; Man., 1940; Sask., 1945; Ont., 1952.

Melilotus alba Desr. (white sweet clover). Isolated from decayed roots. Man., 1934.

Penstemon procerus Dougl. Isolated from diseased parts of wilted plants. Man., 1939.

Phaseolus coccineus L. (scarlet runner). Isolated from the basal parts of plants with foot rot. Man., 1938.

Phaseolus vulgaris L. (kidney bean). Isolated from decayed roots of plants, Man., 1938; from lesions on pods and from discolored seed, Man., 1940.

Phlox drummondii Hook. (annual phlox). Isolated from diseased basal parts. Man., 1941.

Picea pungens Engelm. (blue spruce). Isolated from the roots of blighted seedlings. Sask., 1955.

Pinus banksiana Lamb. (jack pine). Isolated from 2-year-old plants with top necrosis. Sask., 1953.

Pinus resinosa Ait. (red pine). Isolated from damped-off seedlings. Ont. and Sask., 1953.

Pinus sylvestris L. (Scots pine). Isolated from damped-off seedlings, Sask., 1951; from 1- and 2-year-old plants with top necrosis. Sask., 1953.

Pisum sativum L. (pea). Isolated from the diseased basal parts of seedlings in a greenhouse and from adult plants in the field. Man., 1937.

Poa palustris L. (fowl meadow grass). Isolated from decayed roots. Man., 1938.

Poa pratensis L. (Kentucky bluegrass). Isolated from snow mold patches in the spring. Man., 1947.

Populus tremuloides Michx. (American aspen). Isolated from decayed wood. N.B., 1952.

Populus sp. (poplar). Isolated from a cankered twig. Sask., 1942.

Pontentilla monspeliensis L. (rough cinquefoil). Isolated from discolored basal parts of plants. Man., 1938.

Prinsepia sinensis Oliver (prinsepia). Isolated from plants that had become moldy in storage. Sask., 1953.

Prunus spp. Isolated from the fruit of the Compass cherry, Man., 1942; from the roots of plum seedlings following winter injury, Man., 1949.

Rheum rhaponticum L. (rhubarb). Isolated from decayed petioles of rhubarb. Man., 1945.

Sagittaria latifolia Willd. (broad-leaved arrowhead). Isolated from the basal parts of plants. Man., 1938.

Salix sp. (willow). Isolated from sporodochia on blighted leaves. Northwest Territories, 1940.

Salpiglossis sinuata Ruis & Pav. (painted tongue). Isolated from the decayed basal parts of plants. Man., 1941.

Sambucus racemosa L. (European red elder). Isolated from discolored and decayed wood of main stem and secondary shoots exhibiting wilt, Man., 1945; from dying twigs, Sask., 1953.

Secale cereale L. (rye). Isolated from diseased basal parts. Man., 1932.

Sempervivum tectorum L. (houseleek). Isolated from decayed basal parts of plants growing in a greenhouse. Man., 1944.

Sisymbrium altissimum L. (tumbling mustard). Isolated from the basal parts of plants. Man., 1938.

Solanum melongena L. var. *esculentum* Nees (eggplant). Isolated from a decayed fruit. Man., 1944.

Solanum tuberosum L. (potato). Isolated from the stolons and roots of wilted plants, Man., 1939; from decayed tubers in storage along with *Fusarium coeruleum* (Lib.) Sacc., Man., 1943; Ont., 1952.

Spinacia oleracea L. (spinach). Isolated from basal parts of wilted plants. Man., 1941.

Thalictrum venulosum Trel. (veiny meadow rue). Isolated from discolored basal parts of plants. Man., 1938.

Trifolium pratense L. (red clover). Isolated from decayed roots. Que., 1954.

Triticum aestivum L. (common wheat). Isolated from diseased basal parts, Man., 1932; from snow mold of winter wheat, B.C., 1951; from blighted heads, Man. and Ont., 1937; Sask., 1942.

Triticum durum Desf. (durum wheat). Isolated from diseased basal parts of plants with white heads, Man., 1932; from blighted heads of Khapli wheat, Man., 1948.

Tulipa gesneriana L. (tulip). Isolated from a blighted leaf tip, Man., 1939; from decayed bulbs and roots of plants that had died prematurely, along with *Cylindrocarpon radicicola* Wr., Man., 1941.

Ulmus americana L. (American elm). Isolated from discolored twigs. Que., 1948.

Vicia faba L. (broad bean). Isolated from decayed stem bases. Man., 1941.

Vicia sativa L. (common vetch). Isolated from decayed roots of Monantha vetch. Man., 1939.

Zea mays L. (corn). Isolated from sporodochia on overwintered corn stubble. Man., 1935.

INSECTS

Hypera punctata (F.) (clover-leaf weevil). Isolated from dead weevils. Man., 1948.

Melanoplus bivittatus (Say) (two-striped grasshopper). Isolated from diseased and from apparently healthy eggs. Man., 1938.

FUSARIUM EQUISETI (Cda.) Sacc.

Wollenweber and Reinking, Die Fusarien, pp. 63–64. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 173. 1950.
Gordon, Can. J. Botany, 30: 225–226. 1952.

Syn. *F. roseum* Lk. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.

F. roseum Lk. emend. Snyder & Hansen f. *cerealis* (Cke.) Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663–664. 1945.

F. gibbosum App. & Wr. emend. Bilai
Bilai, The Fusaria, pp. 261–263. 1955.

PLANTS

Aegilops hybrid. Isolated from diseased basal parts of plants growing in a greenhouse. Man., 1955.

Agropyron pauciflorum (Schwein.) Hitchc. (slender wheat grass). Isolated from diseased basal parts. Sask., 1937.

Agropyron smithii Rydb. (blue couch grass). Isolated from blighted heads. Sask., 1935.

Agrostis palustris Huds. (creeping bent). Isolated from lesions on the leaves; from plants with snow mold of the horticultural variety Washington bent. Ont., 1951.

Antirrhinum majus L. (snapdragon). Isolated from discolored basal parts. Man., 1937.

Asparagus officinalis L. var. *altilis* L. (asparagus). Isolated from occasional plants with foot rot and premature yellowing of aboveground parts. Man., 1938.

Avena sativa L. (oat). Isolated from diseased roots and other basal parts, Man., 1932; from blighted spikelets of Beaver oats, N.S., 1951.

Begonia tuberhydrida Voss (tuberous begonia). Isolated from diseased tubers. Man., 1939.

Beta vulgaris L. (sugar beet). Isolated from discolored and shrunken roots. Man., 1932.
Bromus inermis Leyss. (brome grass). Isolated from diseased basal parts. Man., 1933.
Callistephus chinensis Nees (China aster). Isolated from discolored basal parts. Man., 1934.
Capsicum frutescens L. (red pepper). Isolated from the basal parts of wilted plants. Man., 1938.
Caragana arborescens Lam. (caragana). Isolated from damped-off seedlings. Sask., 1952.
Chenopodium album L. (lamb's-quarters). Isolated from the basal parts. Man., 1938.
Chrysanthemum sp. (chrysanthemum). Isolated from diseased basal parts. Man., 1938.
Cucumis melo L. var. *cantalupensis* Naud. (cantaloupe). Isolated from fruit with a stem-end rot. Man., 1938.
Cucumis sativus L. (cucumber). Isolated from green fruits with a soft rot. This species was apparently the cause of extensive damage to stored cucumbers in a pickle factory in the autumn. Isolates proved to be pathogenic through wounds to green cucumber fruits in laboratory tests. Man., 1933; from the vascular tissue of wilted cucumber vines, Man., 1937; from fruit following damage by hail, Man., 1938.
Cucurbita pepo L. (pumpkin). Isolated from stored pumpkins with dry rot. Man., 1940.
Dahlia pinnata Cav. (dahlia). Isolated from discolored stems and buds. Man., 1940.
Daucus carota L. var. *sativa* DC. (carrot). Isolated from shrunken and decayed tap roots. Man., 1937.
Dianthus barbatus L. (sweet William). Isolated from discolored basal parts of wilted plants. Man., 1939.
Dianthus caryophyllus L. (carnation). Isolated from diseased basal parts of wilted plants. B.C., 1946.
Hordeum jubatum L. (squirreltail grass). Isolated from discolored basal parts. Sask., 1933.
Hordeum vulgare L. (barley). Isolated from diseased basal parts. Man., 1932.
Ipomoea batatas Lam. (sweet potato). Isolated from decayed areas in imported tubers. Ont., 1935.
Lathyrus odoratus L. (sweet pea). Isolated from diseased basal parts. Man., 1932.
Linum usitatissimum L. (flax). Isolated from basal parts of blighted seedlings and mature plants, Man., 1932; Ont., 1934; Sask., 1948; Que., 1949.
Lolium temulentum L. (darnel). Isolated from discolored roots. Sask., 1933.
Lupinus hirsutus L. (blue lupine). Isolated from decayed basal parts. N.S., 1936.
Lupinus polyphyllus Lindl. (lupine). Isolated from lesions on cotyledons of seedlings growing in a greenhouse. Man., 1938.
Lycopersicum esculentum Mill. (tomato). Isolated from decayed areas in green fruit. Isolates proved to be pathogenic to green fruit when inoculated through wounds. Man., 1932.
Melilotus alba Desr. (white sweet clover). Isolated from decayed roots. Man., 1934.
Papaver rhoeas L. (Shirley poppy). Isolated from decayed basal parts. Man., 1938.
Pastinaca sativa L. (parsnip). Isolated from basal parts of wilted plants. Man., 1938.
Phaseolus vulgaris L. (kidney bean). Isolated from diseased basal parts, Man., 1934; from anthracnose lesions on the pods, Man., 1940.
Picea glauca Voss (white spruce). Isolated from damped-off seedlings. Sask., 1953.
Pinus banksiana Lamb. (jack pine). Isolated from damped-off seedlings. Sask., 1955.
Pinus resinosa Ait. (red pine). Isolated from damped-off seedlings. Ont., 1953.
Pinus sylvestris L. (Scots pine). Isolated from damped-off seedlings. Sask., 1953.
Pisum sativum L. (pea). Isolated from a leaf spot, Man., 1935; from plants with root rot in the greenhouse and in the field, Man., 1938.
Portulaca grandiflora Hook. (rose moss). Isolated from seed. Sask., 1950.
Prunus armeniaca L. (apricot). Isolated from decayed roots of seedlings. Man., 1941.
Prunus besseyi Bailey (western sandcherry). Isolated from decayed roots following winter injury. Man., 1936.
Prunus persica Batsch (peach). Isolated from rhizosphere of seedlings. Ont., 1953.
Rubus ideaus L. (red raspberry). Isolated from a plant with blue stem. Que., 1955.
Salix sp. (willow). Isolated from sporodochial masses on surface of leaves. Northwest Territories, 1940.
Sambucus racemosa L. (European red elder). Isolated from discolored wood of twigs with dieback. Sask., 1953.
Setaria viridis (L.) Beauv. (green foxtail). Isolated from discolored basal parts. Man., 1935.

Solanum melongena L. var. *esculentum* Nees (eggplant). Isolated from discolored basal parts of wilted plants. Man., 1938.

Solanum tuberosum L. (potato). Isolated from sporodochia on the surface of decayed tubers. Man., 1939.

Spinacia oleracea L. (spinach). Isolated from sporodochia on infected crowns of plants destroyed by a foot rot, Man., 1940; from plants with stem blackening and wilt, Ont., 1952.

Syringa vulgaris L. (lilac). Isolated from decayed roots. Sask., 1942.

Triticum aestivum L. (common wheat). Isolated from diseased basal parts of seedlings and adult plants, Man., 1932; from blighted heads, Man., 1933; Ont. and Que., 1937; Alta., 1941; Sask., 1942.

Triticum durum Desf. (durum wheat). Isolated from diseased basal parts of plants, Man., 1932; from blighted heads, Man., 1942.

Zea mays L. (corn). Isolated from basal parts of blighted seedlings, Man., 1936; from sporodochia on overwintered corn stalks, Man., 1949; from seed that failed to germinate, Man., 1951; from a stalk rot, Ont., 1951.

INSECTS

Camnula pellucida (Scudd.) (clear-winged grasshopper). Isolated from diseased eggs. Man., 1941.

Hypera punctata (F.) (clover-leaf weevil). Isolated from dead weevils. Man., 1948.

Section Discolor Wr.

Wollenweber and Reinking, Die Fusarien, pp. 69–72. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 197. 1950.
Gordon, Can. J. Botany, 30: 227. 1952.
Syn. Section Discolor Wr. emend. Bilai pr. p.
Bilai, The Fusaria, pp. 259–261. 1955.

Four species, one variety, and one form of *Fusarium*, namely *F. culmorum* (W. G. Sm.) Sacc., *F. graminearum* Schwabe, *F. heterosporum* Nees emend. Raillo, *F. sambucinum* Fuckel, *F. samb.* var. *coeruleum* Wr., and *F. samb.* form 6 Wr., classified in this section of the genus, were isolated from plants. *F. culmorum*, *F. heterosporum*, and *F. sambucinum* were isolated also from insects. None was isolated from fungi.

Fusarium culmorum (W. G. Sm.) Sacc.

Wollenweber and Reinking, Die Fusarien, pp. 79–81. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 212. 1950.
Bilai, The Fusaria, p. 269. 1955.
Syn. *F. discoloriformis* Raillo
Raillo, Fungi of the genus *Fusarium*, p. 180. 1950.
F. sambucinum Fuckel var. *cereale* (Cke.) Raillo
Raillo, Fungi of the genus *Fusarium*, p. 211. 1950.
F. sambucinum Fuckel emend. Bilai pr. p.
Bilai, The Fusaria, p. 266. 1955.
F. culmorum (W. G. Sm.) Sacc. emend. Bilai pr. p.
Bilai, The Fusaria, p. 269. 1955.

PLANTS

Agropyron pauciflorum (Schwein.) Hitchc. (slender wheat grass). Isolated from discolored basal parts. Sask., 1937.

Antirrhinum majus L. (snapdragon). Isolated from basal parts of wilted plants. Man., 1954.

Avena sativa L. (oat). Isolated from diseased basal parts of adult plants, Man., 1932; from blighted leaves of plants growing in a greenhouse, Man., 1935; from basal parts of plants with prematurity blight, Man., 1946; from blighted spikelets, N. S., 1951.

Bromus inermis Leyss. (brome grass). Isolated from basal parts of diseased plants. Man., 1932.
Caragana arborescens Lam. (caragana). Isolated from blighted seedlings. Sask., 1953.
Chenopodium album L. (lamb's-quarters). Isolated from the roots of apparently healthy plants. Man., 1938.
Dactylis glomerata L. (orchard grass). Isolated from the crowns and basal leaves of plants with dieback. Ont., 1952.
Dianthus caryophyllus L. (carnation). Isolated from the basal parts of diseased plants in a nursery. Ont., 1952.
Hordeum vulgare L. (barley). Isolated from basal parts of adult plants with foot rot, Man., 1932; B. C. 1938; from blighted heads, N. S., 1938; Man., 1948.
Linum usitatissimum L. (flax). Isolated from diseased roots. Sask., 1933.
Medicago lupulina L. (black medick). Isolated from roots of a dead plant. Ont., 1951.
Medicago sativa L. (alfalfa). Isolated from diseased basal parts. Alta., 1935: Ont., 1952.
Pisum sativum L. (pea). Isolated from basal parts of plants with foot rot. Man., 1942.
Rosa sp. (rose). Isolated from a plant with collar rot. Que., 1955.
Solanum tuberosum L. (potato). Isolated from stems of plants suspected of having *Fusarium* wilt. Man., 1943.
Triticum aestivum L. (common wheat). Isolated from diseased basal parts in the field, Man., 1932; Sask., 1936; from basal parts of blighted plants growing in a greenhouse, Man., 1954; from blighted heads, Man. and Ont., 1935; P. E. I., 1938; Alta., 1941; B. C., 1942; N. S., 1950; from wheat stubble, Fort Simpson, N. W. T., 1953.
Triticum durum Desf. (durum wheat). Isolated from diseased basal parts, Man., 1932; Sask., 1938; from blighted heads, Man., 1935; Ont., 1948.
Viola tricolor L. var. *hortensis* DC. (pansy). Isolated from the basal parts of a wilted plant. B. C., 1947.
Zea mays L. (corn). Isolated from blighted seedlings, Man., 1936; from diseased roots of adult plants, Ont., 1952.

INSECTS

Hypera punctata (F.) (clover-leaf weevil). Isolated from dead weevils. Man., 1947.

FUSARIUM GRAMINEARUM Schwabe

Wollenweber and Reinking, Die Fusarien, pp. 82–83. 1935.
Raillo, Fungi of the genus *Fusarium*, pp. 213–214. 1950.
Bilai, The Fusaria, p. 264. 1955.
Syn. *F. roseum* Lk. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.
F. roseum Lk. emend. Snyder & Hansen f. *cerealis* (Cke.) Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663–664. 1945.

PLANTS

Avena sativa L. (oat). Isolated from panicles with head blight, Que., 1939; from ascospores taken from mature perithecia of *Gibberella zeae* (Schw.) Petch on oat stubble, Ont., 1953; N. S., 1958.
Hordeum vulgare L. (barley). Isolated from spikes with head blight. Que., 1949.
Secale cereale L. (rye). Isolated from spikes with head blight. Que., 1938.
Triticum aestivum L. (common wheat). Isolated from spikes with head blight, P. E. I. and N. S., 1938; Ont. and N. B., 1940; Man., 1942; Que., 1946; from basal parts of plants with foot rot, Man., 1950.
Triticum dicoccum Schrank. (emmer). Isolated from spikes with head blight, P. E. I., 1940; Que., 1948.
Triticum durum Desf. (durum wheat). Isolated from spikes with head blight. Que., 1955.
Zea mays L. (corn). Isolated from ascospores taken from mature perithecia of *Gibberella zeae* (Schw.) Petch produced on overwintered corn stubble. Man., 1948.

FUSARIUM HETEROSPORUM Nees emend. Raillo (Fig. 2)

Raillo, Fungi of the genus *Fusarium*, pp. 216–217. 1950.
Wollenweber and Reinking, Die Fusarien, pp. 72–73. 1935.
Bilai, The Fusaria, pp. 264–265. 1955.

Syn. *F. reticulatum* Mont.
Wollenweber and Reinking, Die Fusarien, p. 73. 1935.
F. reticulatum Mont. f. 1 Wr.
Wollenweber and Reinking, Die Fusarien, p. 74. 1935.
F. heterosporum Nees v. *congoense* Wr.
Wollenweber and Reinking, Die Fusarien, p. 73. 1935.

PLANTS

Pinus monticola Dougl. (western white pine). Isolated from a canker on a branch. B. C., 1949.
Rosa sp. (rose). Isolated from sporodochia on a cankered twig. Ont., 1949.

INSECTS

Adelges piceae (Ratz.) (balsam woolly aphid). Isolated from a dead aphid. N. B., 1949.

FUSARIUM SAMBUCINUM Fuckel

Wollenweber and Reinking, Die Fusarien, pp. 75–76. 1935.
Raillo, Fungi of the genus *Fusarium*, pp. 208–209. 1950.
Syn. *F. roseum* Lk. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.

PLANTS

Avena sativa L. (oat). Isolated from diseased basal parts. Man., 1935.
Chenopodium album L. (lamb's-quarters). Isolated from apparently healthy roots. Man., 1938.
Crataegus ? *oxycantha* L. (English hawthorn). Isolated from a canker on a branch. Ont., 1948.
Cucumis melo L. var. *cantalupensis* Naud. (cantaloupe). Isolated from fruit with a stem-end rot. Man., 1938.
Helianthus annus L. (sunflower). Isolated from basal parts of blighted seedlings growing in a greenhouse. Man., 1953.
Hordeum vulgare L. (barley). Isolated from diseased basal parts. Man., 1935.
Linum usitatissimum L. (flax). Isolated from blighted seedlings in a greenhouse. Man., 1940.
Phaseolus vulgaris L. (kidney bean). Isolated from diseased basal parts. B. C., 1945.
Picea pungens Engelm. (blue spruce). Isolated from basal parts of a diseased seedling. Sask., 1953.
Pinus banksiana Lamb. (jack pine). Isolated from damped-off seedlings. Sask., 1953.
Prunus armeniaca L. (apricot). Isolated from roots of blighted seedlings. Man., 1941.
Prunus sp. (plum). Isolated from decayed roots. Man., 1951.
Rubus idaeus L. (red raspberry). Isolated from a wilted plant. Que., 1934.
Solanum tuberosum L. (potato). Isolated from decayed tubers in storage, Ont., 1934; Man. and B. C., 1951.
Triticum aestivum L. (common wheat). Isolated from diseased basal parts. Man., 1935.
Triticum durum Desf. (durum wheat). Isolated from diseased basal parts. Man., 1935.

INSECTS

Chilocorus stigma (Say) (twice-stabbed ladybeetle). Ont., 1953.
Melanoplus bivittatus (Say) (two-striped grasshopper). Isolated from diseased eggs. Man., 1946.

FUSARIUM SAMBUCINUM Fuckel var. COERULEUM Wr.

Wollenweber, Ann. Mycol. 15: 55. 1917.
Gordon, Can. J. Botany, 30: 227 and 230. 1952.
Syn. *F. sambucinum* Fuckel f. 1 Wr.
Wollenweber, Fusarium-Monographie, p. 356. 1931.
Wollenweber and Reinking, Die Fusarien, pp. 76–77. 1935.
F. roseum Lk. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.
F. sambucinum Fuckel f. 2 Wr.
Wollenweber, Fusarium-Monographie, p. 357. 1931.
Wollenweber and Reinking, Die Fusarien, p. 77. 1935.

PLANTS

Canna generalis Bailey (canna). Isolated from rotted roots taken from plants growing in a greenhouse. Man., 1938.
Fragaria chiloensis Duchesne var. *ananassa* Bailey (cultivated strawberry). Isolated from diseased roots. N. S., 1940.
Hordeum vulgare L. (barley). Isolated from blighted heads of the variety Velvet. Que., 1949.
Larix sibirica Ledeb. (Siberian larch). Isolated from damped-off seedlings. Sask., 1953.
Linum usitatissimum L. (flax). Isolated from diseased basal parts. B. C., 1944.
Medicago sativa L. (alfalfa). Isolated from diseased roots. Man., 1951.
Melilotus alba Desr. (white sweet clover). Isolated from diseased basal parts. Man., 1936.
Pinus banksiana Lamb. (jack pine). Isolated from blighted seedlings. Sask., 1955.
Pinus contorta Loud. var. *latifolia* Wats. (lodgepole pine). Isolated from damped-off seedlings. B. C., 1949.
Pseudotsuga taxifolia Britt. (Douglas fir). Isolated from damped-off seedlings. B. C., 1949.
Solanum tuberosum L. (potato). Isolated from abnormally enlarged lenticels of tubers. Ont., 1942.
Triticum aestivum L. (common wheat). Isolated from a spike with head blight. Que., 1937.

FUSARIUM SAMBUCINUM Fuckel form 6 Wr.

Wollenweber and Reinking, Die Fusarien, p. 78. 1935.
Gordon, Can. J. Botany, 30: 230–231. 1952.
Syn. *F. trichothecioides* Wr.
Wollenweber, Fusarium-Monographie, pp. 367–368. 1931.
Wollenweber and Reinking, Die Fusarien, p. 85. 1935.
F. roseum Lk. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 32: 663. 1945.
F. sambucinum Fuckel form 3 Raillo
Raillo, Fungi of the genus *Fusarium*, p. 210. 1950.
F. sambucinum Fuckel var. *trichothecioides* (Wr.) Bilai
Bilai, The Fusaria, p. 268. 1955.

PLANTS

Solanum tuberosum L. (potato). Isolated from tubers with dry rot, Man., 1933; Alta. and Que., 1935; Sask., 1940; P. E. I., 1941; B. C., 1950; N. B., 1951; from the roots and from the stem 2 in. above ground of a wilted potato plant, Man., 1933.

Section Liseola Wr., Sherb., Rg., Johann, and Bailey

Wollenweber and Reinking, Die Fusarien, pp. 96–98. 1935.
Raillo, Fungi of the genus *Fusarium*, pp. 257–258. 1950.
Syn. Section Elegans Wr. emend. Bilai pr. p.
Bilai, The Fusaria, pp. 279–280. 1955.

F. moniliforme Sheld. and its variety *subglutinans* Wr. & Rg., belonging in this section of the genus, were isolated from relatively few species of plants. Only the variety *subglutinans* was isolated from insects.

FUSARIUM MONILIFORME Sheld.

Wollenweber and Reinking, Die Fusarien, pp. 98–99. 1935.
Snyder and Hansen, Am. J. Botany, 32: 664. 1945.
Raillo, Fungi of the genus *Fusarium*, pp. 260–261. 1950.
Syn. *F. moniliforme* Sheld. var. *minus* Wr.
Wollenweber and Reinking, Die Fusarien, p. 102. 1935.
F. lactis Pir. & Rib.
Wollenweber and Reinking, Die Fusarien, p. 103. 1935.
F. moniliforme Sheld. var. *lactis* (Pir. & Rib.) Bilai
Bilai, The Fusaria, pp. 283–284. 1955.

PLANTS

Allium cepa L. (onion). Isolated from pinkish blotched areas of mature seed stalks. Man., 1939.

Caragana arborescens Lam. (caragana). Isolated from the stems of dead seedlings. Sask., 1953.

Pinus sylvestris L. (Scots pine). Isolated from damped-off seedlings. Sask., 1952.

Prunus persica Batsch (peach). Isolated from the rhizosphere of seedlings. Ont., 1953.

Triticum aestivum L. (common wheat). Isolated from the diseased base of a plant. Man., 1932.

Zea mays L. (corn). Isolated from plants with a reddish-pink nodal rot and ear shank rot, Man., 1939; from blighted seedlings in a greenhouse, Man., 1941; from decayed roots of dent corn, Ont., 1949; from conidial masses on overwintered corn stalks, Man., 1949.

FUSARIUM MONILIFORME Sheld. var. SUBGLUTINANS Wr. & Rg.

Wollenweber and Reinking, Die Fusarien, p. 100. 1935.
Snyder and Hansen, Am. J. Botany, 32: 664. 1945.
Bilai, The Fusaria, p. 283. 1955.

Syn. *F. neoceras* Wr. & Rg.
Wollenweber and Reinking, Die Fusarien, pp. 103–104. 1935.

F. neoceras Wr. & Rg. var. *subglutinans* (Wr. & Rg.) Raillo
Raillo, Fungi of the genus *Fusarium*, p. 263. 1950.

PLANTS

Zea mays L. (corn). Isolated from ears and stalks. Ont., 1957.

INSECTS

Pyrausta nubilalis (Hbn.) (European corn borer). Isolated from dead larvae in corn stalks. Ont., 1940.

Section Lateritium Wr.

Wollenweber and Reinking, Die Fusarien, pp. 86–88. 1935.
Gordon, Can. J. Botany, 30: 231–232. 1952.
Raillo, Fungi of the genus *Fusarium*, pp. 264–268. 1950.

Syn. Section Discolor Wr. emend. Bilai pr. p.
Bilai, The Fusaria, pp. 259–261. 1955.

One species, namely *F. lateritium*, classified in this section of the genus, was isolated occasionally from plants, once from a fungus, but not from insects.

FUSARIUM LATERITIUM Nees

Wollenweber and Reinking, Die Fusarien, pp. 88–90. 1935.
Snyder and Hansen, Am. J. Botany, 32: 664. 1945.
Raillo, Fungi of the genus *Fusarium*, pp. 268–270. 1950.
Bilai, The Fusaria, pp. 265–266. 1955.

Syn. *F. lateritium* Nees var. *mori* Desm.
Wollenweber and Reinking, Die Fusarien, pp. 91–92. 1935.

PLANTS

Citrus sinensis Osbeck (sweet orange). Isolated from pinkish mycelium associated with a decay of imported fruit. Man., 1949.

Euonymus alatus Sieb. Isolated from sporodochia present on a branch canker. B. C., 1940.

Fraxinus pennsylvanica Marsh. var. *lanceolata* Sarg. (green ash). Isolated from mycelial tufts on overwintered twigs. Man., 1941.

Hibiscus syriacus L. (rose of Sharon). Isolated from sporodochia on a dead branch. Ont., 1948.

Juglans nigra L. (black walnut). Isolated from a branch canker. B. C., 1943.

Laburnum watereri Dipp. (laburnum). Isolated from sporodochia on a branch. Ont., 1948.

Morus alba L. (white mulberry). Isolated from sporodochia on blighted twigs. B. C., 1942.

FUNGI

Saccharomyces cerevisiae Meyen (yeast). Isolated from a discolored commercial yeast culture. Man., 1940.

Section Elegans Wr.

Wollenweber and Reinking, Die Fusarien, pp. 104–109. 1935.
Snyder and Hansen, Am. J. Botany, 27: 64–67. 1940.
Raillo, Fungi of the genus *Fusarium*, pp. 238–246. 1950.
Gordon, Can. J. Botany, 30: 236. 1952.
Bilai, The Fusaria, pp. 279–280. 1955.

Syn. Section Elegans Wr. emend. Bilai pr. p.
Bilai, The Fusaria, p. 279. 1955.

The only species, namely *F. oxysporum* Schl. emend. Snyder & Hansen, and its one variety, *redolens* (Wr.) Gordon, now included in this section of the genus, were isolated commonly from plants and occasionally from insects. Fourteen pathogenic formae of *F. oxysporum* were isolated from plants only. Isolates of *Fusarium* belonging in this section were not obtained from fungi.

FUSARIUM OXYSPORUM Schl. emend. Snyder & Hansen

Wollenweber and Reinking, Die Fusarien, pp. 117–118. 1935.
Snyder and Hansen, Am. J. Botany, 27: 66. 1940.
Raillo, Fungi of the genus *Fusarium*, p. 239. 1950.
Bilai, The Fusaria, pp. 280–282. 1955.

Syn. *F. oxysporum* Schl. emend. Snyder & Hansen var. *orthoceras* (App. & Wr.) Bilai
Bilai, The Fusaria, p. 282. 1955.

PLANTS

Agropyron sp. Isolated from the roots. Ont., 1934.
Allium cepa L. (onion). Isolated from pink roots. Ont., 1953.
Amaranthus retroflexus L. (pigweed). Isolated from apparently healthy roots. Man., 1938.
Anemone canadensis L. (meadow anemone). Isolated from apparently healthy basal parts. Man., 1938.
Antirrhinum majus L. (snapdragon). Isolated from discolored basal parts of wilted plants in a garden, Man., 1937; from damped-off seedlings in the greenhouse, Man., 1938.
Artemisia biennis Willd. (biennial wormwood). Isolated from apparently healthy roots. Man., 1938.
Asclepias syriaca L. (silky milkweed). Isolated from apparently healthy roots. Man., 1938.
Asparagus officinalis L. var. *altilis* L. (asparagus). Isolated from diseased basal parts, Sask., 1933; from the basal parts of prematurely yellowed plants, Man., 1937: from lesions on roots, Ont., 1949.
Avena sativa L. (oat). Isolated from diseased basal parts. Man., 1932.
Canna generalis Bailey (canna). Isolated from diseased basal parts of plants growing in a greenhouse. Man., 1938.
Caragana arborescens Lam. (caragana). Isolated from discolored basal parts of wilted and dead plants. Man., 1932.
Chenopodium album L. (lamb's-quarters). Isolated from the basal parts of apparently healthy plants. Man., 1938.
Chrysanthemum sp. (chrysanthemum). Isolated from diseased basal parts, Man., 1938; from wilted plants, B. C., 1949.
Clarkia elegans Dougl. (clarkia). Isolated from diseased basal parts. Man., 1941.
Cosmos bipinnatus Cav. (cosmos). Isolated from diseased basal parts of wilted plants. Man., 1936.
Cucumis melo L. var. *cantalupensis* Naud. (cantaloupe). Isolated from roots and basal parts of wilted plants. Man., 1938.

Cucumis sativus L. (cucumber). Isolated from discolored basal parts of wilted plants. Man., 1938.
Cucurbita maxima Duchesne (squash). Isolated from lesions on the cotyledons of Green Hubbard seedlings. B. C., 1945.
Cucurbita pepo L. (vegetable marrow). Isolated from the basal parts of wilted plants. Man., 1938.
Dahlia pinnata Cav. (dahlia). Isolated from discolored lesions on the buds. Man., 1934.
Daucus carota L. var. *sativa* DC. (carrot). Isolated from shrivelled fine roots of plants infected with aster yellows. Man., 1935.
Dianthus barbatus L. (sweet William). Isolated from the basal parts of plants with foot rot and wilt. Man., 1932.
Dianthus caryophyllus L. (carnation). Isolated from diseased basal parts of wilted plants. Man., 1941.
Erysimum cheiranthoides L. (wormseed mustard). Isolated from apparently healthy roots. Man., 1938.
Fragaria chiloensis Duchesne var. *ananassa* Bailey (cultivated strawberry). Isolated from the roots of diseased plants. N. S., 1940.
Fuchsia hybrida Voss (garden fuchsia). Isolated from decayed roots. Man., 1946.
Gaillardia aristata Pursh (gaillardia). Isolated from the basal parts of apparently healthy plants. Man., 1938.
Galium boreale L. (northern bedstraw). Isolated from discolored roots. Man., 1938.
Gaura coccinea Nutt. (scarlet gaura). Isolated from the basal parts of apparently healthy plants. Man., 1938.
Glycine max Merr. (soybean). Isolated from lesions on the roots. Man., 1934.
Hibiscus syriacus (rose of Sharon). Isolated from sporodochia on the basal parts of stem, and crown. Ont., 1955.
Hordeum jubatum L. (squirreltail grass). Isolated from lesions on the roots. Sask., 1933.
Hordeum vulgare L. (barley). Isolated from diseased basal parts, Man., 1932, and B. C., 1938; from blighted leaves, Sask., 1949.
Hyacinthus orientalis L. (hyacinth). Isolated from decayed bulbs, Man., 1935; from blighted buds, Man., 1953.
Impatiens balsamina L. (garden balsam). Isolated from discolored roots. Man., 1941.
Lathyrus odoratus L. (sweet pea). Isolated from the basal parts of plants with severe foot rot. Man., 1944.
Lavatera ? trimestris L. (lavatera). Isolated from discolored crowns and roots. Man., 1941.
Lepidium apetalum Willd. (pepper grass). Isolated from apparently healthy roots. Man., 1938.
Lilium longiflorum Thunb. var. *eximium* Baker (Easter lily). Isolated from discolored stems along with *Botrytis elliptica* (Berk.) Cooke. Man., 1937.
Limonium sinatum Mill. (statice). Isolated from diseased basal parts. Man., 1941.
Linum usitatissimum L. (flax). Isolated from rhizosphere of Novelty flax, Ont., 1939; from blighted seedlings along with *Rhizoctonia solani* Kühn, Man., 1940; from diseased basal parts of adult plants, B. C., 1944.
Lolium temulentum L. (darnel). Isolated from diseased basal parts. Sask., 1933.
Lupinus hirsutus L. (blue lupine). Isolated from the crown and tap root of a wilted plant, N. S., 1936; from diseased basal parts, Man., 1937.
Lupinus polyphyllus Lindl. (lupine). Isolated from lesions on cotyledons of plants growing in a greenhouse. Man., 1937.
Lycopersicum esculentum Mill. (tomato). Isolated from decayed areas of imported fruit. This isolate was pathogenic to green fruit through wounds. Man., 1941.
Malope trifida Cav. (malope). Isolated from decayed crowns and roots. Man., 1940.
Medicago sativa L. (alfalfa). Isolated from lesions on seedlings growing in a greenhouse, Sask., 1948; from plants showing partial winter killing, dwarfing, and a general reduced growth, Ont., 1952.
Melilotus alba Desr. (white sweet clover). Isolated from diseased basal parts. Man., 1934, and Ont., 1945.
Mentzelia lindleyi Torr. & Gray. Isolated from diseased basal parts. Man., 1945.
Monarda menthaefolia Benth. (mint-leaved bergamont). Isolated from apparently healthy roots. Man., 1938.
Nigella damascena L. (love-in-a-mist). Isolated from diseased basal parts. Man., 1938.

Papaver rhoeas L. (Shirley poppy). Isolated from plants with foot rot. Man., 1938.
Pastinaca sativa L. (parsnip). Isolated from the basal parts of wilted plants. Man., 1938.
Penstemon procerus Dougl. Isolated from discolored basal parts. Man., 1939.
Phaseolus coccineus L. (scarlet runner). Isolated from plants with foot rot. Man., 1941.
Phaseolus vulgaris L. (kidney bean). Isolated from sporodochia on lesions on the roots. Man., 1935, and Ont., 1956.
Phlox drummondii Hook. (annual phlox). Isolated from diseased basal parts. Man., 1941.
Picea glauca Voss (white spruce). Isolated from damped-off seedlings. Sask., 1953, and Man., 1955.
Picea pungens Engelm. (blue spruce). Isolated from damped-off seedlings. Ont., 1949.
Pinus banksiana Lamb. (jack pine). Isolated from blighted seedlings. Sask., 1955.
Pinus resinosa Ait. (red pine). Isolated from blighted seedlings. Ont., 1948.
Pinus sylvestris L. (Scots pine). Isolated from blighted seedlings. Sask., 1952.
Pisum sativum L. (pea). Isolated from basal parts of wilted plants. Sask., 1933; Man., 1934; N. S., 1939.
Prunus besseyi Bailey (western sandcherry). Isolated from basal parts of plants following winter injury. Man., 1949.
Prunus persica Batsch (peach). Isolated from the rhizosphere of seedlings. Ont., 1953.
Rheum rhaponticum L. (rhubarb). Isolated from decayed petioles along with *Colletotrichum erumpens* Sacc. Man., 1946.
Rhus toxicodendron L. (poison ivy). Isolated from decayed roots. Man., 1942.
Rubus idaeus L. (red raspberry). Isolated from roots of wilted plants. Que., 1934.
Salpiglossis sinuata Ruis & Pav. (painted tongue). Isolated from decayed roots. Man., 1939.
Salvia splendens Sello (scarlet sage). Isolated from the basal parts of diseased plants. Ont., 1952.
Secale cereale L. (rye). Isolated from the basal parts of diseased plants. Man., 1932.
Sisymbrium altissimum L. (tumbling mustard). Isolated from discolored basal parts. Man., 1938.
Solanum tuberosum L. (potato). Isolated from decayed tubers, Que., 1935, and Man., 1956; from diseased roots, Sask., 1937; from shallow cortical lesions on the stem base, Ont., 1939.
Sonchus arvensis L. (perennial sow thistle). Isolated from discolored roots. Man., 1938.
Spinacia oleracea L. (spinach). Isolated from diseased basal parts of wilted plants. Man., 1941.
Tagetes erecta L. (African marigold). Isolated from diseased roots of wilted plants. Man., 1938.
Thalictrum rugosum Ait. Isolated from diseased basal parts. Man., 1937.
Thalictrum venulosum Trel. (veiny meadow rue). Isolated from apparently healthy roots. Man., 1938.
Trifolium hybridum L. (alsike clover). Isolated from the roots. B. C., 1952.
Trifolium pratense L. (red clover). Isolated from blighted seedlings, Ont., 1953; from diseased roots of mature plants, Que., 1954.
Triticum aestivum L. (common wheat). Isolated from diseased roots, Man., 1932, and N. S., 1953; from blighted heads, Man., 1937.
Triticum durum Desf. (durum wheat). Isolated from diseased basal parts. Man., 1932, and Sask., 1938.
Tulipa gesneriana L. (tulip). Isolated from decayed bulbs, Man., 1938; from the decayed roots of bulbs of the variety William Pitt that died prematurely, Man., 1941; from blind buds, B. C., 1946.
Ursinia pulchra N. E. Br. Isolated from diseased basal parts. N. S., 1939.
Vicia faba L. (broad bean). Isolated from decayed roots and from lesions on the base of the stem. Man., 1937.
Vicia sativa (common vetch). Isolated from diseased basal parts of Monantha vetch. Man., 1939.
Zea mays L. Isolated from blighted seedlings, Man., 1936; from rotted cobs, Man., 1942; from diseased roots of adult plants, Ont., 1949.
Zinnia linearis Benth. Isolated from the basal parts of wilted plants. Man., 1938.

INSECTS

Erannis tiliaria (Harr.) (linden looper). Ont., 1949.
Ipimorpha pleonectusa Grt. Ont., 1949.
Melanoplus bivittatus (Say) (two-striped grasshopper). Isolated from diseased, and from apparently healthy, eggs. Man., 1938.
Pristiphora erichsonii (Htg.) (larch sawfly). Ont., 1949.
Pristiphora geniculata (Htg.) (mountain ash sawfly). N. B., 1954.

FUSARIUM OXYSPORUM Schl. emend. Snyder & Hansen var. REDOLENS (Wr.) Gordon

Raillo, Fungi of the genus *Fusarium*, p. 257. 1950.
Gordon, Can. J. Botany, 30: 238. 1952.
Syn. *F. redolens* Wr.
Wollenweber and Reinking, Die Fusarien, pp. 126–127. 1935.
F. oxysporum Schl. emend. Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 27: 66. 1940.
Section Elegans, Subsection Pseudomartiella
Raillo, Fungi of the genus *Fusarium*, p. 257. 1950.
F. solani (Mart.) App. & Wr. var. *redolens* (Wr.) Bilai
Bilai, The Fusaria, p. 288. 1955.

PLANTS

Antirrhinum majus L. (snapdragon). Isolated from basal parts of wilted plants of the variety Rich Crimson. Man., 1939.
Asparagus officinalis L. var. *altilis* L. (asparagus). Isolated from diseased basal parts of plants with premature yellowing. Man., 1937.
Avena sativa L. (oat). Isolated from diseased roots. Man., 1932.
Brassica napobrassica Mill. (swede). Isolated from tap roots with dry rot. Man., 1945.
Caragana arborescens Lam. (caragana). Isolated from diseased basal parts of adult plants in hedges, Man., 1934; from blighted seedlings in a greenhouse, Sask., 1953.
Caragana pygmaea DC. Isolated from basal parts of wilted seedlings growing in a greenhouse. Man., 1943.
Cucumis melo L. var. *cantalupensis* Naud. (cantaloupe). Isolated from diseased basal parts of wilted plants. Man., 1938.
Cucumis sativus L. (cucumber). Isolated from vascular tissue of the roots from wilted plants. Man., 1940; B. C., 1948.
Cucurbita pepo L. (vegetable marrow). Isolated from diseased basal parts of wilted plants. Man., 1938.
Dahlia pinnata Cav. (dahlia). Isolated from blighted buds. Man., 1934.
Daucus carota L. var. *sativa* L. (carrot). Isolated from shrivelled tap roots. Man., 1935.
Dianthus caryophyllus L. (carnation). Isolated from diseased basal parts of wilted plants. Man., 1935.
Glycine max Merr. (soybean). Isolated from discolored roots. Man., 1934.
Hordeum vulgare L. (barley). Isolated from diseased basal parts of plants. Man., 1932; B. C., 1938.
Lathyrus odoratus L. (sweet pea). Isolated from decayed roots. Man., 1951.
Limonium sinuatum Mill. (statice). Isolated from the roots of wilted plants. Man., 1938.
Linum usitatissimum L. (flax). Isolated from blighted seedlings along with *Rhizoctonia solani* Kühn. Man., 1938.
Lupinus hirsutus L. (blue lupine). Isolated from discolored roots. Man., 1937.
Matthiola incana R. Br. (stock). Isolated from diseased basal parts of wilted plants. Man., 1938.
Medicago sativa L. (alfalfa). Isolated from basal parts of blighted seedlings. Sask., 1948.
Melilotus alba Desr. (white sweet clover). Isolated from diseased basal parts, Man., 1934; from blighted seedlings, Sask., 1949.
Pastinaca sativa L. (parsnip). Isolated from diseased basal parts of shrunken plants. Man., 1935.
Phaseolus vulgaris L. (kidney bean). Isolated from the basal parts of stunted plants. Man., 1934.

Picea glauca Voss (white spruce). Isolated from damped-off seedlings. Sask., 1953; Man., 1955.
Pinus banksiana Lamb. (jack pine). Isolated from blighted seedlings. Man. and Sask., 1955.
Pinus sylvestris L. (Scots pine). Isolated from damped-off seedlings. Sask., 1955.
Pisum sativum L. (pea). Isolated from diseased basal parts of plants in the field and greenhouse. Man., 1940.
Pseudotsuga taxifolia Britt. (Douglas fir). Isolated from damped-off seedlings. B. C., 1949.
Secale cereale L. (rye). Isolated from diseased basal parts. Man., 1932.
Solanum tuberosum L. (potato). Isolated from basal parts of wilted plants, Man., 1939; from decayed tubers in storage, Man., 1940; B. C., 1951.
Tagetes patula L. (French marigold). Isolated from basal parts. Man., 1939.
Thalictrum rugosum Ait. Isolated from diseased basal parts of wilted plants. Man., 1937.
Triticum aestivum L. (common wheat). Isolated from diseased basal parts of prematurely ripened plants. Man., 1932.
Triticum durum Desf. (durum wheat). Isolated from diseased basal parts. Man., 1932; Sask., 1938.
Tulipa gesneriana L. (tulip). Isolated from leaves with tip decay and from bulbs with a basal rot. Man., 1939.
Vicia faba L. (broad bean). Isolated from diseased basal parts. Man., 1937.
Vicia sativa L. (common vetch). Isolated from diseased basal parts of Monantha vetch. Man., 1939.
Zea mays L. (corn). Isolated from roots of blighted seedlings. Man., 1936.
Zinnia linearis Benth. (zinnia). Isolated from diseased basal parts. Man., 1939.

INSECTS

Hypera punctata (F.) (clover-leaf weevil). Isolated from dead weevils. Man., 1946.

FUSARIUM OXYSPORUM Schl. form BETAE (Stewart) Snyder & Hansen

Snyder and Hansen, Am. J. Botany, 27: p. 66. 1940.
Bilai, The Fusaria, p. 281. 1955.

Syn. *F. conglutinans* Wr. var. *betae* Stewart
Stewart, Phytopathology, 21: 59–70. 1931.
Wollenweber and Reinking, Die Fusarien, p. 110. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 249. 1950.

PLANTS

Beta vulgaris L. (mangel). Isolated from diseased seedlings. Ninety per cent of seedlings were killed. N. S., 1942.

FUSARIUM OXYSPORUM Schl. form CALLISTEPHI (Beach) Snyder & Hansen

Snyder and Hansen, Am. J. Botany, 27: p. 66. 1940.
Bilai, The Fusaria, p. 281. 1955.

Syn. *F. conglutinans* Wr. var. *callistephi* Beach
Beach, Mich. Acad. Sci. Report, 20: pp. 281–308. 1918.
Wollenweber and Reinking, Die Fusarien, pp. 110–111. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 249. 1950.
F. conglutinans Wr. var. *callistephi* Beach f. 1 Raillo
Raillo, Fungi of the genus *Fusarium*, pp. 249–250. 1950.
F. oxysporum Schl. form 6 Wr.
Wollenweber and Reinking, Die Fusarien, p. 120. 1935.

PLANTS

Callistephus chinensis Nees (China aster). Isolated from the basal parts of wilted plants. Sask., 1934; Man., 1942.

FUSARIUM OXYSPORUM Schl. form CEPAE (Hanz.) Snyder & Hansen

Snyder and Hansen, Am. J. Botany, 27: p. 66. 1940.
Bilai, The Fusaria, p. 281. 1955.

Syn. *F. cepae* Hanz.
Hanzawa, Mycol. Centralblatt. 5: pp. 4–13. 1914.

F. oxysporum Schl. f. 7 Wr.
Wollenweber and Reinking, Die Fusarien, pp. 120–121. 1935.
F. vasinfectum Atk. var. *zonatum* (Sherb.) f. 1 (Lk. & Bail.) Wr.
Wollenweber and Reinking, Die Fusarien, p. 126. 1935.
F. vasinfectum Atk. var. *zonatum* (Sherb.) f. 2 (Lk. & Bail.) Wr.
Wollenweber and Reinking, Die Fusarien, p. 126. 1935.
F. oxysporum var. *cepae* (Hanz.) Raillo
Raillo, Fungi of the genus *Fusarium*, pp. 253–254. 1950.
F. oxysporum Schl. var. *cepae* (Hanz.) f. 1 Raillo
Raillo, Fungi of the genus *Fusarium*, p. 254. 1950.

PLANTS

Allium cepa L. (onion). Isolated from decayed bulbs. B. C., 1933; Man., 1935.

FUSARIUM OXYSPORUM Schl. form CONGLUTINANS (Wr.) Snyder & Hansen

Snyder and Hansen, Am. J. Botany, 27: p. 66. 1940.
Bilai, The Fusaria, p. 281. 1955.
Syn. *F. conglutinans* Wr.
Wollenweber, Phytopathology, 3: pp. 24–50. 1913.
Wollenweber and Reinking, Die Fusarien, p. 110. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 249. 1950.
F. conglutinans Wr. f. 1 Raillo
Raillo, Fungi of the genus *Fusarium*, p. 249. 1950.

PLANTS

Brassica oleracea L. var. *capitata* L. (cabbage). Isolated from basal parts of plants with yellows. Que., 1952.

FUSARIUM OXYSPORUM Schl. form DIANTHI (Prill. & Del.) Snyder & Hansen

Snyder and Hansen, Am. J. Botany, 27: 66. 1940.
Syn. *F. dianthi* Prill. & Del.
Delacroix, Ann. Nat. Agron. 16: 161–201. 1900.
Wollenweber and Reinking, Die Fusarien, pp. 123–124. 1935.
F. oxysporum Schl. var. *dianthi* (Prill. & Del.) Raillo
Raillo, Fungi of the genus *Fusarium*, pp. 255–256. 1950.

PLANTS

Dianthus barbatus L. (sweet William). Isolated from diseased basal parts of wilted plants. Que., 1945.
Dianthus caryophyllus L. (carnation). Isolated from basal parts of wilted plants. Man., 1932.

FUSARIUM OXYSPORUM Schl. form FABAE Yu & Fang

Yu & Fang, Phytopathology, 38: 587–594. 1948.

PLANTS

Vicia faba L. (broad bean). Isolated from wilted plants. Quebec, 1952.

FUSARIUM OXYSPORUM Schl. form GLADIOLI (Massey) Snyder & Hansen

Snyder and Hansen, Am. J. Botany, 27: p. 66. 1940.
Bilai, The Fusaria, p. 281. 1955.
Buxton, Trans. Brit. Mycol. Soc. 38: pp. 193–201. 1955.
Syn. *F. oxysporum* Schl. var. *gladioli* Massey
Massey, Phytopathology, 16: pp. 509–523. 1926.
F. orthoceras Wr. var. *gladioli* McCull.
McCulloch, Phytopathology, 34: pp. 263–287. 1944.

PLANTS

Gladiolus spp. (gladiolus). Isolated from roots and corms of plants with yellows in gardens and from shrunken corms in storage. Man. and Sask., 1935; Ont., 1943.

FUSARIUM OXYSPORUM Schl. form LILII Imle
Imle, Am. Lily Yearbook, pp. 30–41. 1942.

PLANTS

Lilium longiflorum Thunb. (white trumpet lily). Isolated from bulbels with a basal rot of the scales. B. C., 1949.

FUSARIUM OXYSPORUM Schl. form LINI (Bolley) Snyder & Hansen
Snyder and Hansen, Am. J. Botany, 27: p. 66. 1940.
Bilai, The Fusaria, p. 281. 1955.
Syn. *F. lini* Bolley
Bolley, Proc. Twenty-second Ann. Meet. Soc. Prom. Agr. Sci. pp. 1–4. 1901.
Wollenweber and Reinking, Die Fusarien, p. 113. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 250. 1950.

PLANTS

Linum usitatissimum L. (flax). Isolated from the basal parts of wilted plants. Man., 1932; Ont., 1934; Sask., 1939; and Que., 1944.

FUSARIUM OXYSPORUM Schl. form LYCOPERSICI (Sacc.) Snyder & Hansen
Snyder and Hansen, Am. J. Botany, 27: p. 66. 1940.
Bilai, The Fusaria, p. 281. 1955.
Syn. *F. bulbigenum* Cke. & Mass. var. *lycopersici* (Brushi) Wr. & Rg.
Wollenweber and Reinking, Die Fusarien, pp. 114–115. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 252. 1950.

PLANTS

Lycopersicum esculentum Mill. (tomato). Isolated from the basal part of stems of wilted plants. Man., 1938.

FUSARIUM OXYSPORUM Schl. form MELONIS Snyder & Hansen
Snyder and Hansen, Am. J. Botany, 27: p. 66. 1940.
Miller, Can. J. Research, C, 23: pp. 16–43. 1945.
Syn. *F. bulbigenum* Cke. & Mass. var. *niveum* (E.F.S.) Wr. f. 2 Leach & Currence
Leach and Currence, Minn. Agr. Exp. Sta. Tech. Bull. 129. 32 pp. 1938.
F. bulbigenum Cke. & Mass. var. *cucumis* Raillo
Raillo, Fungi of the genus *Fusarium*, p. 252. 1950.

PLANTS

Cucumis melo L. (muskmelon). Isolated from wilted plants. Ont., 1945.

FUSARIUM OXYSPORUM Schl. form NARCISSI Snyder & Hansen
Snyder and Hansen, Am. J. Botany, 27: p. 66. 1940.
Syn. *F. bulbigenum* Cke. & Mass. pr. p.
Wollenweber & Reinking, Die Fusarien, pp. 113–114. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 250. 1950.

PLANTS

Narcissus pseudo-narcissus L. (daffodil, trumpet narcissus). Isolated from imported narcissus bulbs that rotted badly in transit, Sask., 1936; from decayed daffodil bulbs, B.C., 1946.

FUSARIUM OXYSPORUM Schl. form PINI (Hartig) Snyder & Hansen
Snyder and Hansen, Am. J. Botany, 27: 66. 1940.
Syn. *F. oxysporum* Schl. var. *aurantiacum* (Lk.) Wr.
Wollenweber and Reinking, Die Fusarien, pp. 121–122. 1935.
F. oxysporum Schl. var. *aurantiacum* (Lk.) f. 1 Wr.
Wollenweber and Reinking, Die Fusarien, p. 122. 1935.
F. bulbigenum Cke. & Mass. var. *blasticola* (Rostrup) Wr.
Wollenweber and Reinking, Die Fusarien, p. 115. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 251. 1950.
F. oxysporum Schl. f. *blasticola* (Rostrup) Bilai
Bilai, The Fusaria, p. 281. 1955.

PLANTS

Pinus resinosa Ait. (red pine). Isolated from damped-off seedlings. Man., 1937.
Pinus sylvestris L. (Scots pine). Isolated from damped-off seedlings. Ont., 1948.
Pseudotsuga taxifolia Britt. (Douglas fir). Isolated from damped-off seedlings. B.C., 1946.

FUSARIUM OXYSPORUM Schl. form TUBEROSI Snyder & Hansen

Snyder and Hansen, Am. J. Botany, 27: p. 66. 1940.
Syn. *F. oxysporum* Schl. f. 1 Wr.
Wollenweber and Reinking, Die Fusarien, p. 119. 1935.
F. oxysporum Schl. var. *solani* Raillo
Raillo, Fungi of the genus *Fusarium*, p. 254. 1940.
F. oxysporum Schl. f. *solani* Bilai
Bilai, The Fusaria, p. 281. 1955.

PLANTS

Solanum tuberosum L. (potato). Isolated from stems of wilted plants. Man., 1935; B.C., 1945.

Section Martiella Wr.

Wollenweber and Reinking, Die Fusarien, pp. 127–129. 1935.
Raillo, Fungi of the genus *Fusarium*, p. 219. 1950.
Gordon, Can. J. Botany, 30: 238–239. 1952.
Syn. Section Martiella Wr. emend. Bilai pr. p.
Bilai, The Fusaria, pp. 284–285. 1955.

Two species, namely *F. solani* (Mart.) App. & Wr. emend. Snyder & Hansen and *F. coeruleum* (Lib.) Sacc., classified in this section of the genus, were isolated from plants. Only *F. solani* was isolated from insects. Neither species was isolated from fungi. Three pathogenic formae of *F. solani*, namely, f. *eumartii* (Carp.) Snyder & Hansen, f. *phaseoli* (Buck.) Snyder & Hansen, and f. *pisi* (Jones) Snyder and Hansen, were isolated from their respective hosts, *Solanum tuberosum*, *Phaseolus vulgaris*, and *Pisum sativum*.

FUSARIUM SOLANI (Mart.) App. & Wr. emend. Snyder & Hansen

Snyder and Hansen, Am. J. Botany, 28: p. 740. 1941.
Raillo, Fungi of the genus *Fusarium*, pp. 232–233. 1950.
Gordon, Can. J. Botany, 30: pp. 239–240. 1952.
Bilai, The Fusaria, pp. 286–287. 1955.
Syn. *F. solani* (Mart.) App. & Wr. var. *aduncisporum* (Weim. & Hart.) Wr. pr. p.
Bilai, The Fusaria, p. 287. 1955.

PLANTS

Allium cepa L. (onion). Isolated from decayed bulbs of Russian multipliers. Man., 1941.
Ammobium alatum R. Br. (winged everlasting). Isolated from diseased basal parts of wilted plants. Man., 1938.
Antirrhinum majus L. (snapdragon). Isolated from diseased roots of wilted plants. Man., 1937.
Asclepias syriaca L. (silky milkweed). Isolated from basal parts of apparently healthy plants. Man., 1938.
Brassica oleracea L. var. *capitata* L. (cabbage). Isolated from the roots of wilted plants. Sask., 1949.
Bromus inermis Leyss. (brome grass). Isolated from diseased basal parts. Man., 1932.
Canna generalis Bailey (canna). Isolated from rotted basal parts. Man., 1944.
Caragana arborescens Lam. (caragana). Isolated from diseased basal parts of seedling and adult plants. Man., 1932; Sask., 1934.
Carthamus tinctorius L. (safflower). Isolated from diseased basal parts of wilted plants. Man., 1952.

Chrysanthemum sp. (chrysanthemum). Isolated from discolored roots of stunted plants. Man., 1938.
Clarkia elegans Dougl. (clarkia). Isolated from the diseased basal parts of wilted plants. Man., 1941.
Cucumis melo L. var. *cantalupensis* Naud. (cantaloupe). Isolated from basal parts of wilted plants. Man., 1938.
Cucumis sativus L. (cucumber). Isolated from diseased roots. Man., 1940.
Daucus carota L. var. *sativa* DC. (carrot). Isolated from decayed tap roots in storage, Alta., 1932; from decayed fine roots, Man., 1937.
Delphinium ajacis L. emend. J. Gay. (rocket larkspur). Isolated from diseased roots of wilted plants. Man., 1938.
Dianthus caryophyllus L. (carnation). Isolated from diseased basal parts of dead plants. Man., 1953.
Elaeagnus angustifolia L. (Russian olive). Isolated from diseased roots. Sask., 1943.
Euphorbia esula L. (leafy spurge). Isolated from apparently healthy roots. Man., 1938.
Gladiolus sp. (gladiolus). Isolated from decayed roots and corms. Man., 1938; Ont., 1952.
Glycine max Merr. (soybean). Isolated from diseased roots. Man., 1934.
Godetia amoena Don (godetia). Isolated from roots of wilted plants along with *Cylindrocarpon radicicola* Wr. Man., 1940.
Hedera helix L. (English ivy). Isolated from diseased basal parts of imported plants. Man., 1957.
Helianthus annuus L. (sunflower). Isolated from lesions on the tap root and secondary roots. Sask., 1943.
Hieracium canadense Michx. (Canadian hawkweed). Isolated from apparently healthy roots. Man., 1938.
Hordeum vulgare L. (barley). Isolated from diseased basal parts. Man., 1932.
Humulus lupulus L. (European hop). Isolated from diseased roots of imported plants. Man., 1946.
Lathyrus odoratus L. (sweet pea). Isolated from diseased basal parts. Man., 1932.
Lavatera ? trimestris L. (lavatera). Isolated from discolored basal parts. Man., 1941.
Lilium longiflorum Thunb. var. *eximium* Nichols (Easter lily). Isolated from discolored areas of the stems. Man., 1940.
Linum usitatissimum L. (flax). Isolated from the rhizosphere of wilted seedlings. Ont., 1939.
Lotus corniculatus L. (bird's-foot trefoil). Isolated from diseased basal parts. Ont., 1952.
Lupinus hirsutus L. (blue lupine). Isolated from diseased basal parts of wilted plants. Man., 1937.
Lupinus polyphyllus Lindl. (lupine). Isolated from lesions on the cotyledons of seedlings in a greenhouse. Man., 1937.
Lycopersicum esculentum Mill. (tomato). Isolated from decayed fruit. Man., 1943.
Matthiola incana R. Br. (stock). Isolated from diseased basal parts. Man., 1938.
Medicago sativa L. (alfalfa). Isolated from basal parts of winter-injured plants. Ont., 1952.
Melilotus alba Desr. (white sweet clover). Isolated from lesions on the roots. Man., 1934.
Mentzelia lindleyi Torr. & Gray. Isolated from basal parts of dying plants. Man., 1945.
Nigella damascena L. (love-in-a-mist). Isolated from the basal parts of diseased plants. Man., 1938.
Paeonia lactiflora Pall. (peony). Isolated from basal parts of wilted plants. Man., 1935.
Papaver rhoeas L. (Shirley poppy). Isolated from basal parts of diseased plants. Man., 1935.
Pastinaca sativa L. (parsnip). Isolated from decayed tap roots. Ont., 1943.
Pelargonium hortorum Bailey (geranium). Isolated from decayed bases of cuttings. Man., 1938.
Phleum pratense L. (timothy). Isolated from plants with abnormal twisting of leaves and stems. Ont., 1952.
Picea glauca Voss (white spruce). Isolated from the basal parts of blighted seedlings. Sask., 1953; Man., 1955.
Pinus banksiana Lamb. (jack pine). Isolated from the basal parts of diseased seedlings. Man., 1955.
Pinus resinosa Ait. (red pine). Isolated from damped-off seedlings. Ont., 1948.

Pisum sativum L. (pea). Isolated from diseased basal parts. Man., 1932; Ont., 1955.
Prunus armeniaca L. (apricot). Isolated from diseased basal parts of seedlings. Man., 1941.
Prunus persica Batsch (peach). Isolated from the rhizosphere of peach seedlings. Ont., 1957.
Rosa sp. (rose). Isolated from the basal parts of wilted cuttings. Man., 1937.
Rubus idaeus L. (red raspberry). Isolated from plants with blue stem. Que., 1955.
Rudbeckia laciniata L. Isolated from basal parts of apparently healthy plants. Man., 1948.
Salpiglossis sinuata Ruis & Pav. (painted tongue). Isolated from the diseased basal parts of wilted plants. Man., 1941.
Sambucus racemosa L. (European red elder). Isolated from discolored wood of main stem and basal shoots. Man., 1945.
Sempervivum tectorum L. (houseleek). Isolated from diseased basal parts. Man., 1944.
Solanum tuberosum L. (potato). Isolated from decayed tubers. Man., 1936; Ont., 1937.
Tagetes patula L. (French marigold). Isolated from diseased basal parts of wilted plants. Man., 1938.
Thalictrum rugosum Ait. Isolated from diseased basal parts. Man., 1937.
Thalictrum venulosum Trel. (veiny meadow rue). Isolated from diseased basal parts. Man., 1938.
Tradescantia fluminensis Vell. (wandering Jew). Isolated from decayed bases of stem cuttings. Man., 1945.
Trifolium pratense L. (red clover). Isolated from blighted seedlings, Ont., 1953; from decayed roots of adult plants, Que., 1954.
Triticum aestivum L. (common wheat). Isolated from diseased basal parts of seedlings and adult plants. Man., 1932.
Triticum durum (durum wheat). Isolated from diseased basal parts of adult plants. Man., 1932.
Tulipa gesneriana L. (tulip). Isolated from decayed bulbs. Man., 1938.
Ulmus americana L. (American elm). Isolated from chips of wood taken from the trunk, Que., 1939; from the wood and bark, Ont., 1948.
Ursinia pulchra N.E. Br. Isolated from diseased basal parts. N.S., 1939.
Vicia faba L. (broad bean). Isolated from diseased basal parts of wilted plants. Man., 1937.
Zea mays L. (corn). Isolated from roots of blighted seedlings. Man., 1936.
Zinnia elegans Jacq. (zinnia). Isolated from basal parts of wilted plants. B.C., 1936.

INSECTS

Melanoplus bivittatus (Say) (two-striped grasshopper). Isolated from the eggs. Man., 1938.

FUSARIUM SOLANI form EUMARTII (Carp.) Snyder & Hansen

Snyder and Hansen, Am. J. Botany, 28: p. 740. 1941.
Syn. *F. solani* (Mart. pr. p.) App. & Wr. var. *eumartii* (Carp.) Wr. pr. p.
Wollenweber and Reinking, Die Fusarien, p. 138. 1935.

PLANTS

Solanum tuberosum L. (potato). Isolated from tubers with vascular necrosis and with shallow cortical lesions. Ont., 1939.

FUSARIUM SOLANI form PHASEOLI (Burk.) Snyder & Hansen

Snyder and Hansen, Am. J. Botany, 28: p. 740. 1941.
Syn. *F. solani* (Mart.) var. *martii* (App. & Wr.) Wr. f. 3 Snyder.
Wollenweber and Reinking, Die Fusarien, pp. 137–138. 1935.
F. solani (Mart.) App. & Wr. pr. p.
Bilai, The Fusaria, pp. 286–287. 1955.

PLANTS

Phaseolus vulgaris L. (kidney bean). Isolated from diseased basal parts of wilted plants. Man., 1934; Ont., 1956.

FUSARIUM SOLANI form PISI (Jones) Snyder & Hansen

Snyder and Hansen, Am. J. Botany, 28: p. 740. 1941.

Syn. *F. solani* (Mart.) var. *martii* (App. & Wr.) Wr. f. 2 Snyder
Wollenweber and Reinking, Die Fusarien, p. 137. 1935.

F. solani (Mart.) App. & Wr. pr. p.
Bilai, The Fusaria pp. 286–287. 1955.

PLANTS

Pisum sativum L. (peas). Isolated from diseased basal parts and from the stems of wilted plants. Man., 1932; Ont., 1955.

FUSARIUM COERULEUM (Lib.) Sacc.

Wollenweber and Reinking, Die Fusarien, p. 134. 1935.
Wollenweber, Fusarium-Monographie II, pp. 176–178. 1944–45.
Raillo, Fungi of the genus Fusarium, p. 234. 1950.
Gordon, Can. J. Botany, 30: 245. 1952.

Syn. *F. solani* (Mart.) App. & Wr. var. *coeruleum* (Lib.) Bilai
Bilai, The Fusaria, pp. 287–288. 1955.

F. solani (Mart.) App. & Wr. f. *radicicola* (Wr.) Snyder & Hansen pr. p.
Snyder and Hansen, Am. J. Botany, 28: p. 740. 1941.

PLANTS

Solanum tuberosum L. (potato). Isolated from a decay of the tubers in storage. Man.. 1932; Ont., 1934; Que., 1935; Sask., 1942; B.C., 1949; N.B. and P.E.I., 1951; Alta., 1954,

Distribution of Species by Host or Substrate

PLANTS

Acer negundo L. (box elder)
F. sporotrichioides, F. acuminatum

Aegilops hybrid
F. equiseti

Agropyron cristatum (L.) Beauv. (crested wheat grass)
F. acuminatum

Agropyron pauciflorum (Schwein.) Hitchc. (slender wheat grass)
F. poae, F. sporotrichioides, F. acuminatum, F. equiseti, F. culmorum

Agropyron smithii Rydb. (blue couch grass)
F. semitectum, F. equiseti

Agropyron sp.
F. oxysporum

Agrostis palustris Huds. (creeping bent)
F. equiseti

Allium cepa L. (onion)
F. poae, F. avenaceum, F. acuminatum, F. moniliforme, F. oxysporum, F. oxysporum f. *cepae, F. solani*

**Amaranthus retroflexus* L. (pigweed)
F. oxysporum

Ammobium alatum R. Br. (winged everlasting)
F. solani

**Anemone canadensis* L. (meadow anemone)
F. oxysporum

Antirrhinum majus L. (snapdragon)
F. acuminatum, F. equiseti, F. culmorum, F. oxysporum, F. oxysporum var. *redolens, F. solani*

*Denotes a common weed plant.

**Artemisia biennis* Willd. (biennial wormwood)
F. oxysporum

**Asclepias syriaca* L. (silky milkweed)
F. acuminatum, F. oxysporum, F. solani

Asparagus officinalis L. var. *altilis* L. (asparagus)
F. equiseti, F. oxysporum, F. oxysporum var. *redolens*

Avena sativa L. (oat)
F. poae, F. sporotrichioides, F. arthrosporioides, F. avenaceum, F. acuminatum, F. equiseti, F. culmorum, F. graminearum, F. sambucinum, F. oxysporum, F. oxysporum var. *redolens*

Begonia tuberhybrida Voss (tuberous begonia)
F. equiseti

Beta vulgaris L. (*a*, sugar beet; *b*, mangel)
a, F. equiseti; b, F. oxysporum f. *betae*

Betula lutea Michx. (yellow birch)
F. acuminatum

Betula papyrifera Marsh. (paper birch)
F. semitectum

Brassica napobrassica Mill. (swede)
F. acuminatum, F. oxysporum var. *redolens*

Brassica oleracea L. var. *capitata* L. (cabbage)
F. avenaceum, F. oxysporum f. *conglutinans, F. solani*

Bromus inermis Leyss. (brome grass)
F. poae, F. acuminatum, F. equiseti, F. culmorum, F. solani
Callistephus chinensis Nees (China aster)
F. acuminatum, F. equiseti, F. oxysporum f. *callistephi*
Canna generalis Bailey (canna)
F. acuminatum, F. sambucinum var. *coeruleum, F. oxysporum, F. solani*
Capsicum frutescens L. (red pepper)
F. equiseti
Caragana arborescens Lam. (caragana)
F. avenaceum, F. acuminatum, F. equiseti, F. culmorum, F. moniliforme, F. oxysporum, F. oxysporum var. *redolens, F. solani*
Caragana pygmaea DC.
F. oxysporum var. *redolens*
Carthamus tinctorius L. (safflower)
F. acuminatum, F. solani
**Chenopodium album* L. (lamb's quarters)
F. acuminatum, F. equiseti, F. culmorum, F. sambucinum, F. oxysporum
Chrysanthemum sp.
F. acuminatum, F. equiseti, F. oxysporum, F. solani
**Cirsium arvense* (L.) Scop. (Canada thistle)
F. acuminatum
Citrullus vulgaris Schrad. (watermelon)
F. acuminatum
Citrus sinensis Osbeck (sweet orange)
F. lateritium
Clarkia elegans Dougl. (clarkia)
F. oxysporum, F. solani
Cleome spinosa L. (giant spiderflower)
F. acuminatum
Cosmos bipinnatus Cav. (cosmos)
F. oxysporum
Crataegus ? oxycantha L. (English hawthorn)
F. sambucinum
Cucumis melo L. (muskmelon)
F. oxysporum f. *melonis*
Cucumis melo L. var. *cantalupensis* Naud. (cantaloupe)
F. semitectum, F. acuminatum, F. equiseti, F. sambucinum, F. oxysporum, F. oxysporum var. *redolens, F. solani*
Cucumis sativus L. (cucumber)
F. poae, F. acuminatum, F. equiseti, F. oxysporum, F. oxysporum var. *redolens, F. solani*
Cucurbita maxima Duchesne (squash)
F. poae, F. acuminatum, F. oxysporum
Cucurbita pepo L. (*a*, field pumpkin; *b*, vegetable marrow)
a, F. equiseti; b, F. oxysporum, F. oxysporum var. *redolens*
Dactylis glomerata L. (orchard grass)
F. culmorum
Dahlia pinnata Cav. (dahlia)
F. avenaceum, F. equiseti, F. oxysporum, F. oxysporum var. *redolens*
Daphne mezereum L.
F. avenaceum
Daucus carota L. var. *sativa* DC. (carrot)
F. avenaceum, F. acuminatum, F. equiseti, F. oxysporum, F. oxysporum var. *redolens, F. solani*
Delphinium ajacis L. emend. J. Gay. (rocket larkspur)
F. solani
Dianthus barbatus L. (sweet William)
F. equiseti, F. oxysporum, F. oxysporum f. *dianthi*
Dianthus caryophyllus L. (carnation)
F. avenaceum, F. equiseti, F. culmorum, F. oxysporum, F. oxysporum var. *redolens, F. oxysporum* f. *dianthi, F. solani*
Dianthus chinensis L. (rainbow pink)
F. acuminatum
**Dracocephalum parviflorum* Nutt. (false dragonhead)
F. acuminatum
Elaeagnus angustifolia L. (Russian olive)
F. acuminatum, F. solani
**Erysimum cheiranthoides* L. (wormseed mustard)
F. acuminatum, F. oxysporum
**Euphorbia esula* L. (leafy spurge)
F. acuminatum, F. solani
Euonymus alatus Sieb.
F. acuminatum, F. lateritium
Festuca rubra L. (red fescue)
F. poae
Fragaria chiloensis Duchesne var. *ananassa* Bailey (cultivated strawberry)
F. poae, F. avenaceum, F. acuminatum, F. sambucinum var. *coeruleum, F. oxysporum*
Fraxinus pennsylvanica Marsh. var. *lanceolata* Sarg. (green ash)
F. lateritium
Fuchsia hybrida Voss (common garden fuchsia)
F. oxysporum
**Gaillardia aristata* Pursh (gaillardia)
F. oxysporum
**Galium boreale* L. (northern bedstraw)
F. acuminatum, F. oxysporum
**Gaura coccinea* Nutt. (scarlet gaura)
F. oxysporum
Gladiolus spp. (gladiolus)
F. poae, F. concolor, F. acuminatum, F. oxysporum f. *gladioli, F. solani*
Glycine max Merr. (soybean)
F. semitectum, F. acuminatum, F. oxysporum, F. oxysporum var. *redolens, F. solani*

Godetia amoena Don (godetia)
F. solani
Hedera helix L. (English ivy)
F. solani
Helianthus annuus L. (sunflower)
F. acuminatum, F. sambucinum, F. solani
Hibiscus syriacus L. (rose of Sharon)
F. lateritium, F. oxysporum
**Hieracium canadense* Michx. (Canadian hawkweed)
F. solani
**Hordeum jubatum* L. (squirreltail grass)
F. equiseti, F. oxysporum
Hordeum vulgare L. (barley)
F. poae, F. sporotrichioides, F. avenaceum, F. acuminatum, F. equiseti, F. culmorum, F. graminearum, F. sambucinum, F. sambucinum var. *coeruleum, F. oxysporum, F. oxysporum* var. *redolens, F. solani*
Humulus lupulus L. (European hop)
F. solani
Hyacinthus orientalis L. (hyacinth)
F. oxysporum
Impatiens balsamina L. (garden balsam)
F. acuminatum, F. oxysporum
Ipomoea batatas Lam. (sweet potato)
F. equiseti
Juglans cinerea L. (butternut)
F. avenaceum
Juglans nigra L. (black walnut)
F. lateritium
Laburnum watereri Dipp. (laburnum)
F. lateritium
Larix sibirica Ledeb. (Siberian larch)
F. sambucinum var. *coeruleum*
Lathyrus odoratus L. (sweet pea)
F. equiseti, F. oxysporum, F. oxysporum var. *redolens, F. solani*
**Lathyrus venosus* Muhl. (veiny sweet pea)
F. sporotrichioides
Lavatera ? trimestris L. (lavatera)
F. oxysporum, F. solani
**Lepidium apetalum* Willd. (pepper grass)
F. oxysporum
Lilium longiflorum Thunb. (white trumpet lily)
F. oxysporum f. *lilii, F. solani*
Lilium longiflorum Thunb. var. *eximium* Baker (Easter lily)
F. oxysporum
Limonium sinuatum Mill. (statice)
F. oxysporum, F. oxysporum var. *redolens*
Linum usitatissimum L. (flax)
F. poae, F. avenaceum, F. acuminatum, F. equiseti, F. culmorum, F. sambucinum, F. sambucinum var. *coeruleum, F. oxysporum, F. oxysporum* var. *redolens, F. oxysporum* f. *lini, F. solani*
Lolium temulentum L. (darnel)
F. equiseti, F. oxysporum
Lotus corniculatus L. (bird's-foot trefoil)
F. solani
Lupinus hirsutus L. (blue lupine)
F. acuminatum, F. equiseti, F. oxysporum, F. oxysporum var. *redolens, F. solani*
Lupinus polyphyllus Lindl. (lupine)
F. acuminatum, F. equiseti, F. oxysporum, F. solani
Lycopersicum esculentum Mill. (tomato)
F. acuminatum, F. equiseti, F. oxysporum, F. oxysporum f. *lycopersici, F. solani*
Malope trifida Cav. (malope)
F. oxysporum
Malus baccata Borkh. (Siberian crab apple)
F. acuminatum
Malus sylvestris Mill. (apple)
F. poae, F. avenaceum, F. acuminatum
Matthiola incana R. Br. (stock)
F. avenaceum, F. oxysporum var. *redolens, F. solani*
Medicago lupulina L. (black medick)
F. culmorum
Medicago sativa L. (alfalfa)
F. poae, F. avenaceum, F. acuminatum, F. culmorum, F. sambucinum var. *coeruleum, F. oxysporum, F. oxysporum* var. *redolens, F. solani*
Melilotus alba Desr. (white sweet clover)
F. poae, F. avenaceum, F. acuminatum, F. equiseti, F. sambucinum var. *coeruleum, F. oxysporum, F. oxysporum* var. *redolens, F. solani*
Mentzelia lindleyi Torr. & Gray
F. oxysporum, F. solani
**Monarda menthaefolia* Benth. (mint-leaved bergamont)
F. oxysporum
Morus alba L. (white mulberry)
F. lateritium
Narcissus pseudo-narcissus L. (daffodil)
F. oxysporum f. *narcissi*
Nigella damascena L. (love-in-a-mist)
F. oxysporum, F. solani
Paeonia lactiflora Pall. (peony)
F. poae, F. solani
Papaver rhoeas L. (Shirley poppy)
F. equiseti, F. oxysporum, F. solani
Pastinaca sativa L. (parsnip)
F. equiseti, F. oxysporum, F. oxysporum var. *redolens, F. solani*
Pelargonium hortorum Bailey (geranium)
F. solani
Penstemon procerus Dougl.
F. avenaceum, F. acuminatum, F. oxysporum
Phaseolus coccineus L. (scarlet runner)
F. acuminatum, F. oxysporum
Phaseolus vulgaris L. (kidney bean)
F. acuminatum, F. equiseti, F. sambucinum, F. oxysporum, F. oxysporum var. *redolens, F. solani* f. *phaseoli*

Phleum pratense L. (timothy)
F. avenaceum, F. solani
Phlox drummondii Hook. (annual phlox)
F. acuminatum, F. oxysporum
Picea glauca Voss (white spruce)
F. equiseti, F. oxysporum, F. oxysporum var. *redolens, F. solani*
Picea pungens Engelm. (blue spruce)
F. acuminatum, F. sambucinum, F. oxysporum
Pinus banksiana Lamb. (jack pine)
F. sporotrichioides, F. acuminatum, F. equiseti, F. sambucinum, F. sambucinum var. *coeruleum, F. oxysporum, F. oxysporum* var. *redolens, F. solani*
Pinus contorta Loud. var. *latifolia* Wats. (lodgepole pine)
F. sambucinum var. *coeruleum*
Pinus monticola Dougl. (western white pine)
F. heterosporum
Pinus resinosa Ait. (red pine)
F. poae, F. avenaceum, F. equiseti, F. oxysporum, F. oxysporum f. *pini, F. solani*
Pinus sylvestris L. (Scots pine)
F. acuminatum, F. equiseti, F. moniliforme, F. oxysporum, F. oxysporum var. *redolens, F. oxysporum* f. *pini*
Pisum sativum L. (pea)
F. avenaceum, F. acuminatum, F. equiseti, F. culmorum, F. oxysporum, F. oxysporum var. *redolens, F. solani, F. solani* f. *pisi*
Poa palustris L. (fowl meadow grass)
F. acuminatum
Poa pratensis L. (Kentucky bluegrass)
F. acuminatum
Populus tremuloides Michx. (American aspen)
F. sporotrichioides, F. acuminatum
Populus sp. (poplar)
F. acuminatum
Portulaca grandiflora Hook. (rose moss)
F. equiseti
**Potentilla monspeliensis* L. (rough cinquefoil)
F. acuminatum
Prinsepia sinensis Oliver (prinsepia)
F. acuminatum
Prunus armeniaca L. (apricot)
F. equiseti, F. sambucinum, F. solani
Prunus besseyi Bailey (western sandcherry)
F. equiseti, F. oxysporum
Prunus persica Batsch (peach)
F. arthrosporioides, F. equiseti, F. moniliforme, F. oxysporum, F. solani
Prunus spp.
F. acuminatum, F. sambucinum
Pseudotsuga taxifolia Britt. (Douglas fir)
F. sambucinum var. *coeruleum, F. oxysporum* var. *redolens*
Rheum rhaponticum L. (garden rhubarb)
F. acuminatum, F. oxysporum
**Rhus toxicodendron* L. (poison ivy)
F. oxysporum
Rosa spp. (rose)
F. culmorum, F. heterosporum, F. solani
Rubus idaeus L. (red raspberry)
F. poae, F. sporotrichioides, F. avenaceum, F. equiseti, F. sambucinum, F. oxysporum, F. solani
Rubus occidentalis L. (blackcap raspberry)
F. avenaceum
**Rudbeckia laciniata* L.
F. solani
**Sagittaria latifolia* Willd. (broad-leaved arrowhead)
F. acuminatum
Salix spp.
F. poae, F. acuminatum, F. equiseti
Salpiglossis sinuata Ruis & Pav. (painted-tongue)
F. acuminatum, F. oxysporum, F. solani
Salvia splendens Sello (scarlet sage)
F. oxysporum
Sambucus racemosa L. (European red elder)
F. poae, F. sporotrichioides, F. avenaceum, F. acuminatum, F. equiseti, F. solani
Secale cereale L. (rye)
F. poae, F. avenaceum, F. acuminatum, F. graminearum, F. oxysporum, F. oxysporum var. *redolens*
Sempervivum tectorum L. (houseleek)
F. acuminatum, F. solani
**Setaria viridis* (L.) Beauv. (green foxtail)
F. equiseti
**Sisymbrium altissimum* L. (tumbling mustard)
F. acuminatum, F. oxysporum
Solanum melongena L. var. *esculentum* Nees (eggplant)
F. acuminatum, F. equiseti
Solanum tuberosum L. (potato)
F. sporotrichioides, F. avenaceum, F. acuminatum, F. equiseti, F. culmorum, F. sambucinum, F. sambucinum var. *coeruleum, F. sambucinum* f. 6, *F. oxysporum, F. oxysporum* var. *redolens, F. oxysporum* f. *tuberosi, F. solani, F. coeruleum*
**Sonchus arvensis* L. (perennial sow thistle)
F. oxysporum
Spinacia oleracea L. (spinach)
F. acuminatum, F. equiseti, F. oxysporum
Symphoricarpos occidentalis Hook. (wolfberry)
F. concolor
Syringa vulgaris L. (lilac)
F. equiseti
Tagetes erecta L. (African marigold)
F. oxysporum

Tagetes patula L. (French marigold)
F. oxysporum var. *redolens*, *F. solani*
Thalictrum rugosum Ait.
F. oxysporum, *F. oxysporum* var. *redolens*, *F. solani*
**Thalictrum venulosum* Trel. (veiny meadow rue)
F. acuminatum, *F. oxysporum*, *F. solani*
Tradescantia fluminensis Vell. (wandering Jew)
F. solani
Trifolium hybridum L. (alsike clover)
F. oxysporum
Trifolium pratense L. (red clover)
F. poae, *F. avenaceum*, *F. acuminatum*, *F. oxysporum*, *F. solani*
Trifolium repens L. (white clover)
F. arthrosporioides, *F. avenaceum*
Triticum aestivum L. (common wheat)
F. poae, *F. sporotrichioides*, *F. avenaceum*, *F. acuminatum*, *F. equiseti*, *F. culmorum*, *F. graminearum*, *F. sambucinum*, *F. sambucinum* var. *coeruleum*, *F. moniliforme*, *F. oxysporum*, *F. oxysporum* var. *redolens*, *F. solani*
Triticum dicoccum Schrank (emmer)
F. poae, *F. graminearum*
Triticum durum Desf. (durum wheat)
F. chlamydosporum, *F. poae*, *F. sporotrichioides*, *F. avenaceum*, *F. acuminatum*, *F. equiseti*, *F. culmorum*, *F. graminearum*, *F. sambucinum*, *F. oxysporum*, *F. oxysporum* var. *redolens*, *F. solani*
Tsuga canadensis Carr. (Canada hemlock)
F. avenaceum
Tulipa gesneriana L. (tulip)
F. poae, *F. acuminatum*, *F. oxysporum*, *F. oxysporum* var. *redolens*, *F. solani*
Ulmus americana L. (American elm)
F. poae, *F. sporotrichioides*, *F. semitectum*, *F. acuminatum*, *F. solani*
Ursinia pulchra N.E. Br.
F. oxysporum, *F. solani*
Vicia faba L. (broad bean)
F. acuminatum, *F. oxysporum*, *F. oxysporum* var. *redolens*, *F. oxysporum* f. *fabae*, *F. solani*
Vicia sativa L. (common vetch)
F. acuminatum, *F. oxysporum*
Viola tricolor L. var. *hortensis* DC. (pansy)
F. culmorum
Zea mays L. (corn)
F. poae, *F. avenaceum*, *F. acuminatum*, *F. equiseti*, *F. culmorum*, *F. graminearum*, *F. moniliforme*, *F. oxysporum*, *F. oxysporum* var. *redolens*, *F. solani*
Zinnia elegans Jacq. (zinnia)
F. solani
Zinnia linearis Benth.
F. oxysporum, *F. oxysporum* var. *redolens*

INSECTS

Actebia fennica (Tausch.) (black army cutworm)
F. arthrosporioides
Adelges piceae (Ratz.) (balsam woolly aphid)
F. heterosporum
Camnula pellucida (Scudd.) (clear-winged grasshopper)
F. equiseti
Carpocapsa pomonella (L.) (codling moth)
F. poae
Chilocorus stigma (Say) (twice-stabbed lady-beetle)
F. sambucinum
Choristoneura fumiferana (Clem.) (spruce budworm)
F. avenaceum
Erannis tiliaria (Harr.) (linden looper)
F. oxysporum
Hypera punctata (F.) (clover-leaf weevil)
F. avenaceum, *F. acuminatum*, *F. equiseti*, *F. culmorum*, *F. oxysporum* var *redolens*
Ipimorpha pleonectusa Grt.
F. oxysporum
Melanoplus bivittatus (Say) (two-striped grasshopper)
F. acuminatum, *F. sambucinum*, *F. oxysporum*, *F. solani*
Musca domestica L. (housefly)
F. poae
Paraclemensia acerifoliella (Fitch) (maple leaf cutter)
F. poae
Pristiphora erichsonii (Htg.) (larch sawfly)
F. poae, *F. oxysporum*
Pristiphora geniculata (Htg.) (mountain ash sawfly)
F. oxysporum
Pyrausta nubilalis (Hbn.) (European corn borer)
F. moniliforme var. *subglutinans*

FUNGI

Melampsora lini (Pers.) Lev.
F. avenaceum
Saccharomyces cerevisiae Meyen
F. lateritium
Ustilago hordei (Pers.) Lagerh.
F. poae
Ustilago kolleri Wille
F. poae

Discussion

As this investigation was continued annually for 25 years and involved a wide range of host plants from an extensive geographic area, the results should present a reasonably complete picture of the species of *Fusarium* that occur in Canada, particularly so when considered in conjunction with the results of concurrent studies by the writer on the species that inhabit agricultural seeds (2, 3, 4) and agricultural soils (5, 6). In fact, practically all of the species of *Fusarium* one might expect to find occurring under the climatic conditions prevailing in Canada have been encountered. Investigation of unusual habitats, such as slime fluxes from cut tree trunks, and from sewage, might however reveal the presence of an additional *Fusarium* species.

The isolation of species of *Fusarium* from insects in Canada is of academic interest but probably of little economic value in the control of the insects from which they are isolated. Certain species of *Fusarium*, namely *F. coccophilum* (Desm.) Wr. & Rg., *F. coccidicola* P. Henn., and *F. larvarum* Fuckel, are known to parasitize scale insects in tropical and subtropical areas, but none of these species was isolated during the present investigation.

F. oxysporum is probably the most important economically of all the species considered, because its specialized pathogenic forms can be destructive to a wide range of cultivated plant species. Fourteen of these pathogenic forms are reported in this paper to occur in Canada, each on a different genus of plants. Undoubtedly others are present and will be encountered in future investigations. These specialized forms are distinguished by their pathogenicity to specific hosts rather than by cultural or morphological characters so that their identification is as much a pathological as a mycological problem. *F. coeruleum* and *F. sambucinum* f. 6 are also of considerable economic importance. They are responsible for important losses of potatoes, particularly in eastern Canada, because of their ability to cause dry rots of tubers in storage. Both species are widely distributed in Canada. The various species that have been reported to occur on cereals have been appraised previously by the writer (3, 4), with respect to their probable role in the production of foot rot and head blight. It needs only to be mentioned here that *F. graminearum* and *F. culmorum* are the most important pathogens of cereals but that *F. avenaceum* also can be a factor in the production of head blight particularly in areas of high atmospheric humidity. As high yield has always been one of the most important criteria employed in the selection of new varieties in the cereal-breeding program, an automatic selective action has doubtless been exerted for resistance to attack by species of *Fusarium* as well as by other pathogenic organisms.

Common weed plants have been shown to harbor species of *Fusarium*. How much importance should be attributed to them in the overwintering and spread of *Fusarium* species, in comparison with trash from cultivated crops, has not been determined but probably should not be disregarded.

Perfect stages are known for several of the species of *Fusarium* found in Canada, although only *Gibberella zeae*, the perfect stage of *F. graminearum*,

has been found in nature by the writer. Further investigations will be required to determine their prevalence in nature in Canada and the role they play in the survival, spread, and variation of their respective *Fusarium* stages.

Acknowledgments

The writer is indebted to Joan A. Harris, who assisted with the more recent culture work and preparation of the manuscript; and to Mr. W. E. Clark, who photographed the drawings. He wishes to express his appreciation to many colleagues in Canadian universities, and in Canada Department of Agriculture research laboratories, who have sent specimens and cultures of *Fusarium* for identification from their respective geographic areas.

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STUDIES IN FOREST PATHOLOGY

XX. INVESTIGATIONS OF THE PATHOLOGICAL DETERIORATION IN KILLED BALSAM FIR[1]

J. T. BASHAM[2]

Abstract

Studies were begun to assess the significance and interrelationships of five fungi consistently associated with the deterioration of balsam fir trees killed by the spruce budworm, and to explain the succession pattern of the fungi in that process. A yeast and *Ophiostoma bicolor* Davidson and Wells were the only fungi consistently isolated from the discolored cambium of dying or recently killed trees; *Stereum chailletii* Pers. and an unidentified hyphomycete, *Fungus F*, were the principal fungi isolated from the stained sapwood of trees dead less than one year; and *Polyporus abietinus* Dicks. ex Fries was the only fungus consistently associated with the rotted sapwood of trees dead for more than one year. A gradual and fairly regular lowering of the moisture content, pH, and strength of balsam fir sapwood from the healthy, living state through the various stages of deterioration was recorded. There was no evidence of marked inhibition or antagonism among the fungi tested in pure culture. Although the most vigorous growth of *P. abietinus* occurred in liquid media adjusted at pH 4.5, compared with 6.5 for *Fungus F* and *S. chailletii*, balsam fir sticks of about pH 6.0 were readily infected by *P. abietinus* in the laboratory. Sticks artificially infected with *S. chailletii* or *P. abietinus* developed a pronounced reddish stain and showed significant reductions in toughness, and the pH of aqueous extracts of these sticks was markedly reduced. The same properties of sticks infected with *Fungus F* differed very little from those of the check sticks. There was no evidence that either *Fungus F* or *S. chailletii* was inhibited by the presence of the other in balsam fir sapwood, or that the presence of either had any effect upon the deteriorating capacity of *P. abietinus*. It is suggested that the principal explanation for the succession pattern of fungi in the deterioration of balsam fir lies in a dependence upon changes in certain properties of the wood substrate, particularly in the moisture content of the sapwood.

Introduction

An estimated 300,000,000 cords of balsam fir (*Abies balsamea* (L.) Mill.) have been destroyed following an unbroken succession of spruce budworm epidemics in eastern Canada during the past 50 years. Killed trees remain for a limited time suitable for pulpwood but the agents of deterioration progressively reduce the yield and quality of the pulp. Assessment of the rate of deterioration has been, therefore, of great economic importance. However, quite apart from this economic incentive, the availability of numerous stands of balsam fir in various stages of deterioration afforded a unique opportunity for a detailed study of the deterioration process.

Several fungi are frequently found associated with deterioration, and with heart rot, in forest trees. An investigation of the rate of deterioration of killed balsam fir, conducted by the author in collaboration with forest entomologists (3, 6), has revealed that the development of sap stain and sap rot in the boles was not the result of a single fungus, as had been generally believed.

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Contribution No. 493 from the Division of Forest Biology, Science Service, Department of Agriculture, Ottawa. Based on a thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy, Queen's University, Kingston, Ontario.
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Although Good[3] has shown that considerable and very variable numbers of fungi may coexist in different stages of heart rot in aspen poplar, *Populus tremuloides* Michx., only five fungi were consistently isolated from the cambium and sapwood of deteriorating balsam fir. These fungi were apparently associated with the deterioration of balsam fir in a more or less regular succession pattern, and a definite relationship was observed between the occurrence of specific fungi and the stage of deterioration. These facts further emphasize the advantages of using dead and dying balsam fir for detailed studies of the wood decay process in nature.

The relatively uniform sequence of fungi in dying and dead balsam fir may result from: (*a*) the ability of the preliminary fungi to reach the substrate sooner than the others; (*b*) competitive or synergistic interactions among the fungi; (*c*) a dependence upon changes in certain properties of the wood substrate; or (*d*) a combination of any two or all three of the above. The object of this study was to determine which of these four statements applied to the succession of fungi in balsam fir, and to assess the significance and interrelationships of the fungi involved.

Few attempts have been made to investigate the complex deterioration process in trees or logs under field conditions, although certain aspects of it have been thoroughly studied. Some of the more pertinent of these reports are reviewed below.

In 1931 Cartwright *et al.* (13) investigated the relationship of losses in mechanical strength, specific gravity, and changes in the chemical composition of wood with the progress of fungal attack under controlled laboratory conditions. They reported that the wood of Sitka spruce (*Picea sitchensis* (Bong.) Carr) attacked by *Trametes serialis* Fr. was altered chemically before there was any loss in wood substance, and that the reduction in strength (modulus of rupture) of the wood was nearly proportional to the degree of decomposition. They concluded that the reduced strength of infected wood was due to alterations of the cell walls, not to a physical breakdown by hyphal penetration, and that changes in the modulus of rupture of the wood constitute a more sensitive measure of the extent of decay than percentage weight losses.

Scheffer (36), in 1936, published a comprehensive account of changes in the physical and chemical properties of red gum (*Liquidambar styraciflua* L.) brought about by the action of *Polyporus versicolor* (L.) Fr. He reported that as decay progressed, all of the strength properties of the wood were reduced more rapidly than was the specific gravity, and that the cell walls were thinned uniformly in advance of the hyphae, presumably by the wood-destroying enzymes of the fungus.

That the complete destruction of wood is often due to a succession of fungi was the basis of a report by Findlay in 1940 (18). He found that the white rot fungus, *P. versicolor*, attacks and completely destroys all components of the wood, whereas fungi in the brown rot group, such as *Coniophora puteana*

[3]Good, H. M. Fungi associated with *Fomes igniarius* (L.) Gill. in decay of poplar. Manuscript filed at Forest Biology Laboratory, Southern Research Station, Maple, Ontario, 1956.

(Schum. ex Fr.) Karst., cannot decompose all of the lignin and were not capable of reducing the original dry weight of infected wood by more than two thirds. Beechwood blocks partially decayed by *P. versicolor* were readily attacked and decomposed by *C. puteana*, but blocks partially rotted by *C. puteana* were decayed very slowly by *P. versicolor*, probably because of the low pH of these blocks. Decay was not accelerated when blocks were previously infected by another fungus of the same group.

Ulbrich (38), in 1941, drew attention to the distinction between stain and rot in the deterioration of trees or timber. He regarded species of *Ophiostoma* as the cause of "blue stain", which does not impair the durability of wood, whereas "sapwood parasites" such as *Stereum* spp. and *Polyporus abietinus*, which frequently accompany or follow the staining fungi, are responsible for the actual decay of the sapwood.

Studies to determine the relation of blue stain to the subsequent development of rotting fungi in Scots pine (*Pinus sylvestris* L.) were published by Björkman in 1947 (9). Sound wood blocks and blocks that had been infected with stain fungi, dried, and sterilized were exposed to several wood-destroying fungi. Percentage weight losses (decay) in the blue-stained blocks and the unstained controls were generally comparable, but it is interesting to note that *P. abietinus* decayed sound wood faster than wood infected with the stain fungus *Ophiostoma piceae* (Münch) Syd. In another experiment fresh pine blocks infected in the laboratory with *O. piceae* were placed directly on cultures of two wood-destroying basidiomycetes. It was estimated visually that the attack of the decay fungi on the control blocks was a little more advanced than on those containing living *O. piceae*, indicating that at least this blue-stain fungus, when active, bestows a degree of protection against certain decay fungi.

Bärlund (2), in 1950, used wood block tests to determine the ability of wood-rotting fungi to live in wood previously decayed or in the process of being decayed. She found no evidence of the production of antibiotics to hinder secondary fungi, and concluded that the effect of the preliminary fungi does not depend on a preventive, poisoning effect, but on impoverishment of the substrate.

Studies of the fungal succession on and in standing and fallen trees have been carried out recently by Mangenot. He reported, in 1954 (26), that wood-rotting basidiomycetes consistently bring about a marked increase in the acidity of aqueous extracts of infected wood. The pH of aqueous extracts of wood infected with blue-stain fungi approached that of sound wood, but when stained wood was subsequently invaded by basidiomycetes its pH was reduced, tending to become fixed at about 4.4. On the other hand, the pH of aqueous extracts of decayed wood subsequently invaded by blue-stain fungi increased.

Whereas the studies reviewed above suggest that interactions of fungi in deterioration may be of importance, only Mangenot's deals with a complex succession and in most the data are derived from experiments on wood which

had been subjected to drastic drying or sterilization procedures. To clarify the mechanisms of the fungal succession in dead balsam fir, the following studies were undertaken:

1. Determination of the symptom progression in deterioration through observations of the macroscopic and microscopic changes in dying and dead balsam fir trees, the relation of insect and fungous attack to tree death, the onset of various phases of deterioration, and descriptions of changes that occur in properties of the wood during the deterioration process.

2. Studies of the fungi associated with deterioration, their distribution in dying and dead trees, relationship to different phases of deterioration, methods of spread and infection, and factors affecting the establishment and activity of these organisms in dying and dead trees.

3. Laboratory studies; the application of new inoculation techniques in assessing the significance of certain changes in the properties of wood during symptom progression to the different fungi associated with deterioration, and in laboratory studies of fungous successions and interactions in balsam fir wood.

The material for most of these studies was obtained from two regions of northwestern Ontario recently or at present subjected to severe spruce budworm infestations. The first lies southwest of Lake Nipigon where the budworm population occurred in epidemic proportions between 1939 and 1948; tree mortality was first observed in 1943. The second area is located in the Kenora and Sioux Lookout districts north of Dryden where mortality was first observed in 1948; this outbreak is still active. One hundred balsam firs were selected, mostly dying trees or trees dead for periods up to 18 months, although a few healthy trees were included. The treatment of samples from these and other trees, and experimental procedures used to test the hypotheses regarding the basis of succession, are described in detail in the appropriate sections below.

The Symptom Progression in Deterioration

Characteristics of Dying and Recently Killed Trees

Balsam fir which have been severely defoliated by spruce budworm differ markedly in appearance from healthy trees. Belyea (8) has described a method of assessing tree vigor and of forecasting impending tree death from a study of the seasonal progress of radial increment and the changes in the foliage during or immediately after the period of severe defoliation. However, with severely defoliated trees it is often difficult to determine if a tree is alive or dead. Dying trees usually have stunted shoots bearing sparse, wilted, yellowish green foliage, whereas any needles on dead trees are as a rule reddish brown in color.

The cambial layer of living balsam fir is pale yellow (Fig. 5) and quite moist in the spring and early summer; it usually remains in this condition until the trees are almost completely defoliated, when it becomes dry and reddish brown. This discoloration of the cambium layer is regarded as a

more reliable indication of tree death than color changes in the foliage. Belyea (8) states, "Discoloration of the cambium is probably not a precise indication of the time of tree death, but it is the first definite, easily observed indication that the tree has reached a condition from which it cannot recover."

Two distinct designs of cambium discoloration were encountered, the particular pattern depending to a great extent upon the population level of the balsam fir bark beetle, *Pityokteines sparsus* Lec. In areas where little or no tree mortality had occurred, that is, the advancing zone of tree mortality, very little bark beetle activity was observed in dying or recently dead trees. This was apparently because of the absence of any appreciable increase in the bark beetle population. Dying trees in these regions generally had moist, pale-yellow cambium until the foliage began to redden, at which time light-brown longitudinal streaks could be detected upon removal of the bark. This was followed eventually by the complete discoloration of the cambium. However, most of the recently killed balsam fir investigated were in areas containing dead trees and therefore large populations of bark beetles which attacked these trees either shortly before or soon after death, frequently while the foliage was still yellowish green. The nuptial chambers and brood galleries formed in the cambium by *P. sparsus* were invariably surrounded by relatively dry, reddish-brown patches in the otherwise moist, pale-yellow cambium (Figs. 1, 2, and 3). Struble, in 1937 (37), reported a similar condition in white fir and red fir attacked by the fir engraver bark beetle, *Scolytus ventralis* Lec., in the western United States. In about four weeks the brown cambial patches in balsam fir had spread until all of the cambium was dry and discolored (Fig. 4). In some trees both types of cambial discoloration outlined above were observed, usually on opposite sides of the trunk.

The distinct relation between insect activity and the pattern of cambium discoloration suggested that insects might play a considerable part in balsam fir deterioration, either as vectors or by mechanically exposing the susceptible tissues of the tree to fungal infection through insect holes in the bark. The bark of most of the trees studied remained intact for at least two years after death. Apart from scattered branch scars, the only openings in the bark of recently killed trees were entrance tunnels of *P. sparsus*. The tunnels were approximately one millimeter in diameter, and densities as high as 50 holes per square foot of bark were often encountered. From 2 months to a year after tree death, these entrance tunnels were augmented by numerous emergence holes of approximately the same size made by the newly formed young adults (7). Egg slits were chewed in the bark of most of the killed trees by the sawyer beetle, or wood borer, *Monochamus scutellatus* Say., at approximately the same time the trees were attacked by bark beetles. The slits, however, left no appreciable openings through the bark. From 1 to 2 years after death, large holes, approximately five millimeters in diameter, were formed in the bark by the emergence of adult sawyer beetles. The significance of these insect holes in deterioration is discussed in a later section of this report, as is the question of the insects serving as vectors.

Phases of Pathological Deterioration

The deterioration of balsam fir killed by the spruce budworm can be separated into three phases, representing three distinctly different conditions of the cambium and sapwood.

The progressive reddish-brown discoloration of the cambium of balsam fir will be referred to as Phase 1 of the deterioration process (Fig. 6). Microscopic plasmolysis tests were made and they showed no living cells in the sapwood of balsam fir following the complete discoloration of the cambium. The sapwood at the end of this phase was nearly always pale-yellow, as was the sapwood of living trees.

Phase 2 consists of a progressive reddening of the sapwood (Figs. 7 and 8). This change in sapwood color is first observed soon after the complete discoloration of the cambium, as a very faint stain of the outer wood, often extending only $\frac{1}{8}$ in. beneath the cambium. During the year following the death of the tree, this stain darkens and penetrates farther towards the center of the bole until practically all of the sapwood has a pronounced yellow-red hue.

Approximately one year after a tree has died, the discolored sapwood, which up to that time has remained firm, begins to soften. The rotted condition of the sapwood will be referred to as Phase 3 (Figs. 9 and 10). The name "pitted sap rot" is often used in referring to this wood, since in the advanced stage it is riddled with small, empty, lens-shaped pockets. The wood can easily be broken and crushed by hand. Sap rot advances annually towards the center of the tree, but at a relatively slow rate so that in trees dissected 5 years after death it rarely extended more than $1\frac{1}{2}$ in. beneath the wood surface.

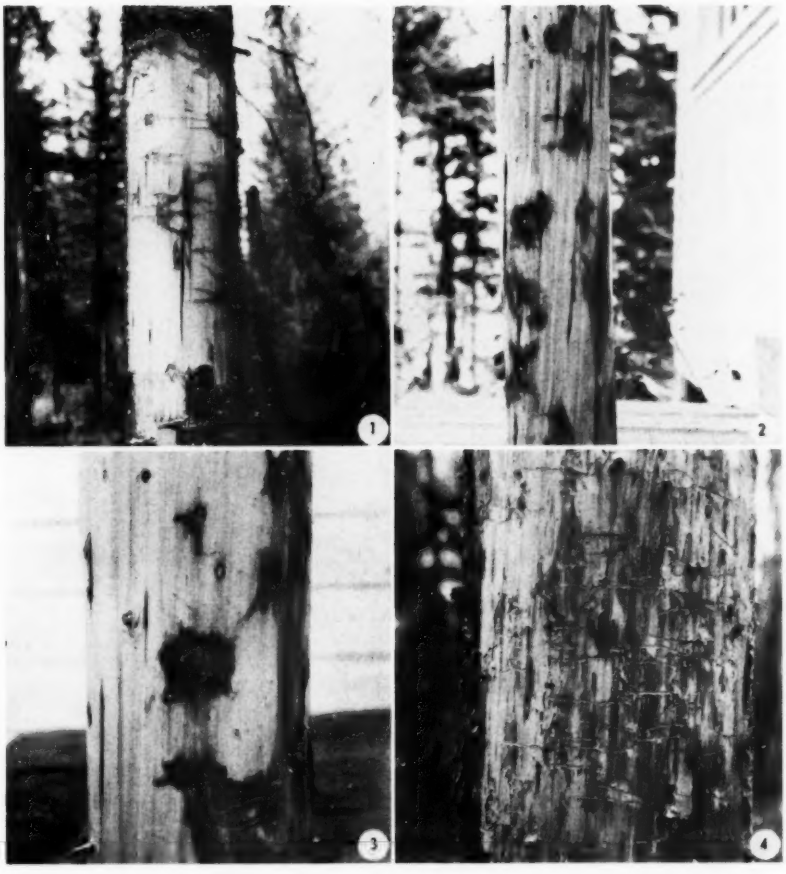
The general pattern of deterioration outlined above was encountered in all of the balsam fir trees examined. Two phases sometimes occurred simultaneously in one tree because of the tendency for one side of the trunk to die earlier than the other. An extreme example was encountered in one tree with sparse yellowish-green foliage. The cambium over one third of the circumference of this tree was alive, whereas sap rot was beginning to develop on the opposite side of the trunk.

Changes in Wood Properties during Deterioration

In the decay of wood, as a rule most, if not all, of the physical and chemical properties of that wood are altered. In this study progressive changes in the color, toughness, moisture content, and pH of balsam fir cambium and sapwood were considered in the hope that the data would help clarify the roles and requirements of the fungi involved in deterioration.

In addition to the gross symptoms of deterioration, changes occurred in the microscopic details of the sapwood of dying and dead trees. Histological studies of this wood and of artificially infected balsam fir sticks were undertaken, but they contributed little to the main objective of this study. They are reported elsewhere (4).

PLATE I



FIGS. 1, 2, and 3. Patches of discolored cambium surrounding bark beetle nuptial chambers and brood galleries in recently killed balsam fir.

FIG. 4. Completely discolored cambium of balsam fir that had been dead for about six weeks.

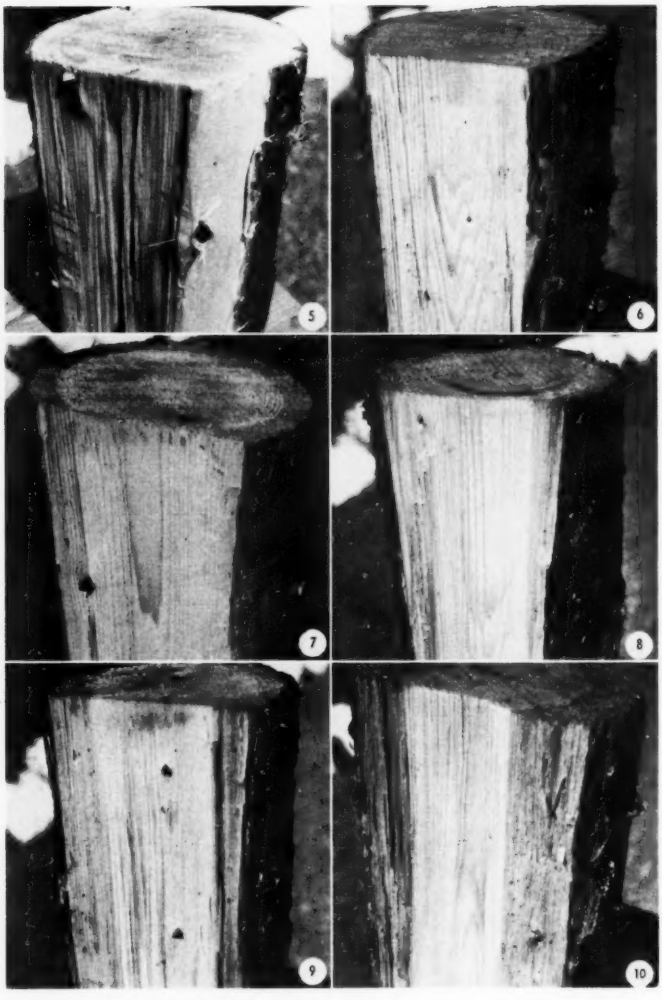


FIG. 5. Section of a living balsam fir.
FIG. 6. Section of a balsam fir in Phase 1 deterioration.
FIG. 7. Section of a balsam fir in Phase 2 deterioration, sapwood lightly stained.
FIG. 8. Section of a balsam fir in Phase 2 deterioration, sapwood deeply stained.
FIG. 9. Section of a balsam fir in Phase 3 deterioration, sapwood moderately soft.
FIG. 10. Section of a balsam fir in Phase 3 deterioration, sapwood very soft and pitted.

Color

The most noticeable change that takes place in balsam fir cambium and sapwood attacked by deteriorating fungi is a change in color. The cambium, which in healthy trees was pale yellow, became reddish brown, and the sapwood changed from pale yellow to yellow-red. To describe these changes accurately, the Munsell book of standard color chips and system of notation was used (30).

Pale-yellow, healthy cambium had a color notation of 2.5Y 8/5, whereas the reddish-brown, discolored cambium surrounding bark beetle galleries was 4.0YR 4/8. In dying or recently killed trees infested with beetles, the boundaries between pale-yellow, healthy cambium and patches of dark-red cambium were very sharp. Gradations between the two colors were seldom observed.

The healthy sapwood in living balsam fir was pale yellow (2.5Y 8.5/4.5), very similar to that of healthy cambium. Lightly stained sapwood in Phase 2 was a deeper yellow (1.5Y 8/6), darkly stained sapwood was yellow-red (9YR 7/7.25), and rotted sapwood in Phase 3 was a slightly redder yellow-red (8.5YR 6.75/9). Hence, as deterioration progressed, all three attributes of the color of the sapwood, hue, value, and chroma, changed progressively. The hue changed from yellow to yellow-red, becoming progressively redder. The value changed from 8.5 to 6.75, that is, it became darker; whereas the chroma (departure from neutral) became progressively stronger, changing from 4.5 in healthy sapwood to 9 in Phase 3.

Toughness

The rotted sapwood of trees dead for 1 year or longer was noticeably softer and weaker than the healthy sapwood of living trees. Faintly stained sapwood in recently killed trees seemed as hard and strong as healthy sapwood. A slight reduction in hardness and strength, however, could be detected in the deeply stained sapwood of some trees in Phase 2. It has been demonstrated that the strength properties of wood constitute a more sensitive measure of the extent of decay than any other easily detectable wood property (13, 32, 36). Several investigations have shown that the toughness and the impact-breaking strength are the easily determined strength properties of wood that are first affected by the action of decay fungi (11, 14, 19, 33, 35). It was decided, therefore, to test the toughness of healthy balsam fir sapwood in different phases and subphases of deterioration, and so determine at what stage of deterioration the actual decay or decomposition of sapwood first becomes significant.

A toughness-testing machine (Fig. 11) was constructed by Mr. R. D. Bradfield in the physics workshop at Queen's University, from a design obtained from the Forest Products Laboratory at Madison, Wisconsin. The bob of the pendulum can be supported at three different positions on the rod. The bob is composed of removable parts so that it can be adjusted to three different weights. The trigger release mechanism can be set so that the pendulum is at an angle of 30, 45, or 60° from the perpendicular as it

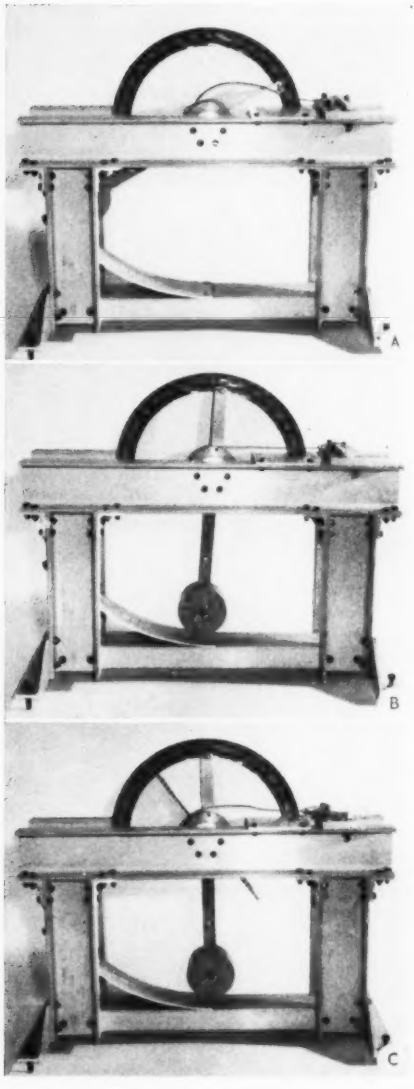


FIG. 11. Toughness-testing machine.
(A) Machine at rest at commencement of test, pendulum and pointer set at 60°.
(B) Pendulum in motion at point of greatest tension upon the test stick.
(C) Completion of test, showing broken test stick and new position of pointer.

commences its downward swing. Thus the machine can be adjusted so that 27 different forces can be applied to break wood sticks.

The machine can be balanced so that the momentum of the pendulum, without encountering any resistance other than the friction inherent in the machine, will propel the pointer from the angle of its initial position to the corresponding angle on the opposite side of the perpendicular. However, if a test stick is placed in the machine and the pendulum started, for example, at 60° from its vertical position (Fig. 11A), a certain amount of energy is absorbed in breaking the stick (Fig. 11B) so that the pointer will not be propelled as far as the 60° mark on the opposite side of the perpendicular (Fig. 11C). The energy in foot-pounds absorbed by the stick, a measure of its toughness, can be determined from the difference between the final angle of the pointer and the initial angle. The energy in foot-pounds required to break test sticks can be obtained from a series of curves for all 27 possible potential energies of the pendulum.

Blocks were collected in the field from the sapwood of living, dying, and dead balsam fir. The dead trees sampled were in all phases and types of deterioration. Small test sticks of similar dimensions, approximately 18 cm × 10 mm × 10 mm, were cut from the blocks, first roughly with a band saw, then more accurately with a thickness planer. The width of the sticks was then measured with micrometer calipers; variations in width up to 0.05 mm between sticks were evident. As this constituted an error of only 0.5% and since other errors inherent in the machine and in the method of sampling could not be corrected, these variations were neglected except for their inclusion in the statistical treatment of the data.

Test sticks were selected as far as possible from wood in which the spacing and angle of the annual rings was similar. No sticks were cut from sections with less than 10 or more than 20 rings per inch, since it has been demonstrated that significant reductions in strength properties are often encountered in wood in which the growth rate has been abnormally slow or abnormally fast (10).

The results of the toughness tests on these sticks are presented in Table I. There was very little reduction in the toughness of balsam fir sapwood until the wood was deeply stained, which occurred approximately three months after death. The toughness of wood in this stage, and of rotted wood, was obviously significantly reduced from that of healthy sapwood and of sapwood in the earlier stages of deterioration.

Moisture Content

Blocks of sapwood, weighing between 200 and 300 g, were cut from living, dying, and dead balsam fir at time of felling. The blocks were immediately wrapped in heavy aluminum foil and sealed with scotch tape to reduce moisture losses to a minimum until they could be weighed. After weighing, the blocks were repeatedly heated at 105° C until their weights remained constant (oven-dry weight). The moisture content was calculated as the percentage of the oven-dry weight.

TABLE I

The relationship between the toughness and the stage of deterioration of balsam fir sapwood sticks

Phase of deterioration	Description of sapwood	Number of test sticks	Average number of annual rings per stick	Average toughness of test sticks with 95% fiducial limits (ft-lb)
	Healthy	11	4.6	3.56 ± 0.34
1	Probably living, from trees with patches of discolored cambium	9	5.8	3.79 ± 0.62
	Dead, no sap stain evident; beneath brown, dry cambium	6	5.0	3.35 ± 0.80
2	Faint sap stain	12	5.1	3.91 ± 0.36
	Medium sap stain	12	5.1	3.12 ± 0.48
	Deep sap stain	6	5.7	2.24 ± 0.48
3	Moderately soft sap rot	8	4.5	1.62 ± 0.68
	Very soft sap rot	11	5.7	1.15 ± 0.14

TABLE II

The relationship between the moisture content and the stage of deterioration of balsam fir sapwood

Phase of deterioration	Description of sapwood	Number of trees sampled	Minimum moisture content,* %	Maximum moisture content,* %	Average moisture content,* %
	Healthy	9	120.9	187.2	145.0
1	Probably living, from trees with patches of discolored cambium	21	97.2	152.8	125.8
	Dead, no sap stain evident; beneath brown, dry cambium	14	53.9	157.1	86.1
2	Faint sap stain	18	56.2	121.1	79.3
	Deep sap stain	23	27.1	126.6	63.4
3	Moderately soft sap rot	14	22.4	124.7	56.8
	Very soft sap rot	5	17.9	79.5	37.5

*Based on ovendry weight.

The results of moisture content calculations are presented in Table II. Despite considerable variations in the moisture contents of the sapwood of balsam fir trees in the same stage of deterioration, a gradual and fairly regular lowering of the moisture content of balsam fir sapwood occurred as it was altered from the healthy, living state through the various stages of deterioration. Whereas the average moisture content of living balsam fir sapwood was approximately 145%, that of sapwood in Phase 3 was reduced to about 50%.

pH

The pH values were determined for aqueous extracts of the cambium layer and sapwood of several of the trees selected for toughness and moisture content studies. The method used was that outlined by Good *et al.* (21). Shavings of the areas to be tested were soaked in distilled water at room temperature. A similar weight of shavings and an equal amount of water were used in each test. Good *et al.* demonstrated that extraction periods of from 1 to 24 hours give substantially the same results. After the shavings had soaked for 4 hours, the pH of the water extracts was determined, using a Beckman pH meter. Although the resultant pH values represent the hydrogen-ion concentrations of water extracts and not of the wood itself, they provide a means of comparing the pH of wood in different stages of deterioration.

The pH of balsam fir cambium and sapwood decreased as deterioration progressed (Table III). The pH of water extracts of the cambium and sapwood of living trees was approximately 6.5, whereas extracts of dead, discolored cambium averaged 5.8, and dead, faintly stained sapwood averaged 5.9. Water extracts of deeply stained sapwood had an average value of 5.5, while visibly rotted sapwood in Phase 3 yielded extracts which were distinctly more acid, with average pH values of 4.5. Not one of the aqueous extracts of 18 samples of sapwood in Phase 3 had a pH value greater than 5.0.

TABLE III

The pH of aqueous extracts of balsam fir cambium and sapwood in different stages of deterioration

Phase of deterioration	Description of sapwood or cambium	Number of samples	Minimum pH	Maximum pH	Average pH
	Healthy sapwood	6	6.3	6.7	6.5
	Healthy cambium	6	6.3	6.6	6.4
1	Cambium healthy in appearance, except for brown patches surrounding bark beetle activity	8	5.9	6.4	6.3
	Dead, brown, dry cambium	10	5.3	6.0	5.8
2	Faintly stained sapwood	8	5.4	6.3	5.9
	Deeply stained sapwood	8	4.6	6.1	5.5
3	Moderately soft, rotted sapwood	12	4.1	5.0	4.6
	Very soft, rotted sapwood	6	4.2	4.9	4.5

The Fungi Associated with Deterioration

Description

Five fungi were consistently isolated from the visibly deteriorated cambium and sapwood of balsam fir killed following spruce budworm defoliation. A malt agar medium was used to isolate the fungi; Good[4] found that none of

[4]Good, H. M. Fungi associated with *Fomes igniarius* (L.) Gill. in decay of poplar. Manuscript filed at Forest Biology Laboratory, Southern Research Station, Maple, Ontario, 1956.

11 other media tested had any advantages over malt agar in isolating a complete range of fungi from decaying poplar wood. Other fungi were occasionally isolated, but so infrequently that their role in the deterioration process of balsam fir must be of minor significance. The five principal fungi were:

1. Yeast

On malt agar this fungus forms slow-growing, pearly white colonies resembling those of bacteria. Photomicrographs are presented in Figs. 12 and 13.

2. Ophiostoma bicolor

This ascomycete was recently described in a paper by Davidson (15).

3. Fungus F

This fungus has not yet been identified. It has tentatively been placed in the genus *Cephalosporium* of the Fungi Imperfecti by Dr. R. F. Cain of the University of Toronto. Its perfect stage, when found, probably will belong in the genus *Ophiostoma* (Figs. 14 and 15).

A cultural description of *Fungus F* follows:

GROWTH CHARACTERS.—Growth moderately rapid, plates usually covered in 3 weeks. Advancing zone even, raised aerial mycelium extending to limit of growth. Mat pale buff (10.0YR 8/3), the newer growth slightly raised and woolly, after 1 week becoming collapsed and thin woolly, with farinaceous surface. Reverse concolorous with colored areas, no odor. On gallic and tannic acid agars no diffusion zones.

HYPHAL CHARACTERS—*Advancing zone:* hyphae hyaline, with simple septa, frequently branched, 2.0–6.0 μ in diameter. *Aerial mycelium:* (*a*) hyphae as in advancing zone, wider hyphae in part with walls slightly thickened and yellow; (*b*) conidia hyaline, one-celled, ovoid to cylindrical, variable in size, 3.0–6.0 $\times$ 1.5–3.5 μ, usually massed on top of conidiophores; (*c*) conidiophores *Cephalosporium*-like, hyaline, tapered, occasionally branched, 25.0–40.0 μ high by 2.0–3.5 μ wide at the base.

4. Stereum chailletii

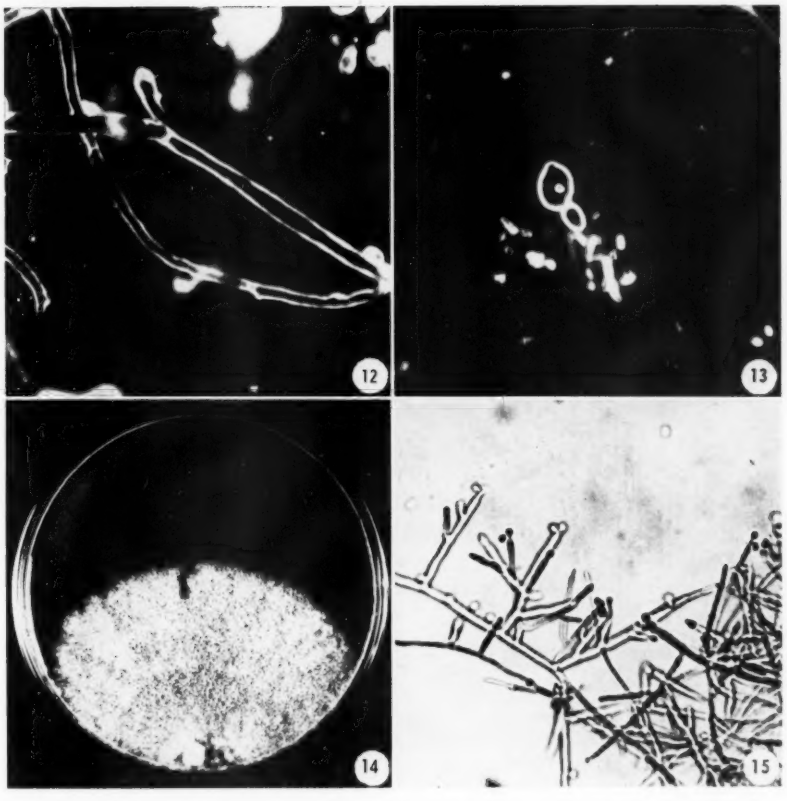
This member of the Basidiomycetes class of fungi has been encountered, but relatively infrequently, in dead coniferous trees in North America. The following cultural description has been made by Dr. M. K. Nobles, Department of Agriculture, Botany and Plant Pathology Division, Ottawa.

GROWTH CHARACTERS.—Growth moderately rapid to slow, plates usually covered in 4 weeks, occasionally in 5 to 6 weeks. Advancing zone even, usually appressed with fibers well separated in narrow zone, rarely slightly raised. Mat white at first and remaining so for 6 weeks or developing extensive pale-buff (10.0YR 8/4) areas in the mycelium or scattered dots, small patches, or incomplete zones yellowish brown (10.0YR 5/6) or reddish brown (5.0YR 5/5) in color, usually at surface of agar and diluted by overgrowth of white mycelium, the newer growth slightly raised, woolly-cottony, so loosely arranged as to be translucent, becoming collapsed, fine woolly, usually with some zones or irregular areas which become felty to pellicular or crustose, compact enough to be opaque, white to colored, occasionally delimited by thong-like strands of compact mycelium grown from surface downwards through agar. Reverse unchanged below white mats, concolorous with colored areas, no odor. On gallic and tannic acid agars diffusion zones moderately strong, no growth or only a trace on gallic acid agar, trace to 2.3 cm diameter on tannic acid agar.

HYPHAL CHARACTERS.—*Advancing zone:* hyphae hyaline, nodose septate, 1.5–4.5 μ in diameter. *Aerial mycelium:* (*a*) hyphae as in advancing zone frequently incrusted with coarse crystals, occasionally with walls greenish yellow in potassium hydroxide; (*b*) cystidia usually numerous in cultures 3 weeks old or older, at first short clavate, thin-walled, usually containing one or two large oil globules, at maturity elongate with thick, refractive walls, greenish yellow to brown, rough, partially incrusted, 3.0–7.5 μ in diameter; (*c*) in crustose areas and thong-like strands, hyphae with branches interlocking to form pseudoparenchymatous layer. *Submerged mycelium:* hyphae as in aerial mycelium, frequently incrusted.

5. Polyporus abietinus

This basidiomycete has been recorded in association with the deterioration of practically every coniferous tree species in North America. A detailed



FIGS. 12 and 13. Photomicrographs of the yeast fungus associated with bark beetles and with discolored balsam fir cambium. (×1150)
FIG. 14. A 2-week-old culture of *Fungus F* grown in the dark on malt agar.
FIG. 15. *Fungus F* (*Cephalosporium* sp.), showing conidiophores and conidia. (×470)

description of this fungus may be obtained from the paper on the identification of cultures of wood-rotting fungi published by Nobles in 1948 (31).

Distribution of the Fungi in Dying and Dead Trees

The three phases of deterioration of the cambium and sapwood of dying and killed balsam fir have been arbitrarily divided into 13 "types". In this way it is possible to present a more detailed account of the occurrence of the five principal fungi associated with deterioration. The 13 types are as follows:

Phase 1

1. Dark-brown discoloration of the cambium surrounding recently formed nuptial chambers and brood galleries of the bark beetle. Remainder of cambium healthy in appearance.
2. Unstained wood immediately beneath the brown cambial patches of type 1.
3. Brown cambium close to healthy cambium where one side or more of the trunk is dead and the remainder appears to be alive.
4. Brown cambium of trees in which no healthy cambium is evident.

Phase 2

5. Very lightly stained sapwood immediately beneath the discolored cambium where one side or more of the trunk is dead and the remainder appears to be alive.
6. Light-red stain of the sapwood.
7. Medium-red stain of the sapwood.
8. Moderately deep red stain of the sapwood.
9. Very deep red stain of the sapwood, wood not noticeably softened.
10. Thin band of deeply stained, firm wood which is often present between rotted Phase 3 sapwood and the central core of sound wood.

Phase 3

11. Pronounced red stain of the sapwood, wood slightly softened.
12. Moderately soft sap rot.
13. Very soft pitted sap rot.

A total of 484 small chips was cut from cambium and sapwood and transferred aseptically to malt agar slants. Fungi from 311 cultures were identified; the remaining cultures were either contaminated, sterile, or yielded fungi which were isolated so infrequently that they were considered of little importance in the deterioration of balsam fir.

Table IV shows the frequency with which the five principal fungi were isolated from cambium and sapwood in the 13 different types, and in the three phases, of deterioration of balsam fir trees. The yeast and *Ophiostoma bicolor* were the only fungi consistently isolated from Phase 1; *Fungus F* and *Stereum chailletii* were the principal fungi isolated from Phase 2; and *Polyporus abietinus* was the only fungus consistently associated with Phase 3. Individual accounts of the occurrence of each of the five fungi in dying and dead balsam fir follow.

TABLE IV

The frequency with which the fungi were isolated from balsam fir cambium and sapwood in different stages of deterioration

Phase of deterioration*	Type of deterioration*	Number of trees cultured	Number of cultures	Number of isolations					Number of cultures identified	Percentage of cultures identified
				Yeast	*Ophiostoma bicolor*	*Fungus F*	*Stereum chailletii*	*Polyporus abietinus*		
1	1	28	100	64	50	2	2	—	69†	69.0
	2	13	31	17	14	2	3	—	23†	74.2
	3	9	13	—	5	4	—	—	9	69.2
	4	13	18	—	10	1	1	—	12	66.7
2	5	19	26	—	1	9	4	—	14	53.8
	6	31	45	—	1	14	14	—	29	64.4
	7	41	66	—	3	14	25	4	46	69.7
	8	30	40	—	4	6	9	5	24	60.0
	9	29	38	—	—	7	10	2	19	50.0
	10	17	19	—	—	7	—	7	14	73.7
3	11	13	18	—	—	—	3	7	10	55.5
	12	15	21	—	—	—	2	10	12	57.1
	13	23	49	—	—	—	—	30	30	61.2
1	1–4		162	81	79	9	6	—	113†	69.8
2	5–10		234	—	9	57	62	18	146	62.4
3	11–13		88	—	—	—	5	47	52	59.1
Totals			484	81	88	66	73	65	311	64.4

*See text for detailed descriptions.
†Sixty-two cultures yielded both yeast and *O. bicolor*.

Yeast.—Isolations of the yeast were limited to patches of discolored cambium surrounding bark beetle activity in dying or recently killed trees, and to wood 1 mm or less beneath these discolored patches.

Ophiostoma bicolor.—This fungus was consistently isolated from the four types of deterioration included in Phase 1, that is, the two types listed above in connection with isolations of the yeast plus the brown cambium of trees in which no healthy cambium was evident. It was occasionally isolated from light to moderately stained sapwood in Phase 2. Apparently, *O. bicolor* is practically confined to the cambium and adjacent wood cells of these trees, and very seldom penetrates any appreciable distance into the wood.

Fungus F.—*Fungus F* was isolated from the 10 types of deterioration included in Phases 1 and 2, but was never isolated from Phase 3. Its occurrence in the four types of deterioration included in Phase 1 was quite sporadic, and most of the isolates of this fungus were obtained from sapwood in Phase 2. Although *Fungus F* was not isolated from the softened sapwood in Phase 3, it was isolated from 7 of the 19 cultures made from the thin band of deeply stained, firm wood often present between rotted Phase 3 sapwood and the central core of sound wood (type 10).

Stereum chailletii.—This fungus was the only one isolated from all three phases of deterioration. Sixty-two of the 73 isolations of *S. chailletii* were from sapwood in Phase 2.

Polyporus abietinus.—*P. abietinus* was obtained from 47 of the 52 identified cultures made from sapwood in Phase 3. It was also isolated 18 times from the more deeply stained types of Phase 2. In earlier studies (3, 6), the writer

reported the occurrence of *P. abietinus* in the sapwood of all balsam fir examined that had been dead for a period of 1 year or longer, but never isolated it from trees that had been dead for shorter periods; sapwood in Phase 3 was found only in trees that had been dead for 1 year or longer. The results of these and the present investigations indicate that *P. abietinus* does not extensively colonize balsam fir that have been dead for less than one year. After this period has elapsed, it apparently becomes quite aggressive and eventually causes the ubiquitous, characteristic "pitted sap rot" of balsam fir.

The relative frequency with which *O. bicolor*, *Fungus F*, *S. chailletii*, and *P. abietinus* were isolated from the cambium and from the sapwood at different depths beneath the cambium of dying and dead balsam fir is illustrated in Fig. 16. *Fungus F* and *S. chailletii* together accounted for approximately the same proportion of the isolations obtained from the cambium and from the sapwood at all of the depths sampled in these trees. A tendency for *Fungus F* to be isolated more frequently than *S. chailletii* at depths greater than 1/16 in. is evident, as is the regular increase in the percentage of isolations of *P. abietinus* with increasing depth. It should be pointed out that the absence of isolations of *P. abietinus* from the cambium is possibly due to the numerous secondary fungi and bacteria which occupied this area during the first year after the death of the trees.

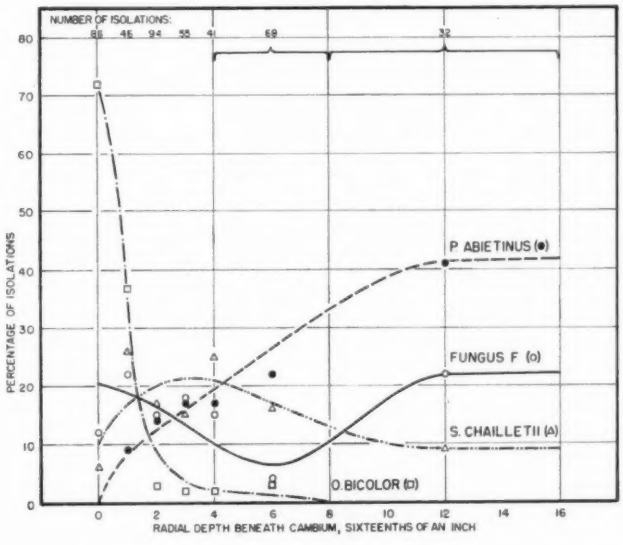


FIG. 16. The frequency with which different fungi were isolated from the cambium and from the sapwood at different depths beneath the cambium of dying and dead balsam fir.

Observations on Spread and Infection

One of the possible hypotheses presented in the Introduction to explain the succession of fungi in deterioration was the ability of the preliminary fungi to reach the substrate before the others. This hypothesis would appear to be particularly plausible if the preliminary fungi are carried by vectors which are able to negotiate the primary barriers to infection.

Investigations and observations of the methods of spread and infection of the fungi have been dealt with in another report (6). It was found that the yeast and *Ophiostoma bicolor* are transmitted by the bark beetle *Pityokteines sparsus*, and *Fungus F* by the wood borer *Monochamus scutellatus*, from dead to dying or very recently killed trees. The spores of *O. bicolor* and *Fungus F* are mucilaginous and not adapted for wind dissemination. Insects have been found to be associated with the spread of such spores and of yeasts (22).

Failure to isolate a specific fungus from one of the insects does not necessarily indicate that that fungus is not transmitted by the insect. The fungus in question may have been dislodged or killed by the surface sterilization treatment of the insect, or suppressed in culture by other fungi or bacteria. Therefore, despite the fact that the basidiospores of the two remaining fungi, *Stereum chailletii* and *Polyporus abietinus*, are not mucilaginous and hence not as likely to be dependent upon insect vectors, it is possible that one or both of them are transmitted in this way. This hardly seems probable in *P. abietinus*, since this fungus was seldom isolated from trees that had been dead for less than one year, and the numerous fructifications throughout the forest would ensure an abundant supply of wind-disseminated spores during the growing season. *S. chailletii*, on the other hand, was consistently isolated from trees that had been killed very recently, although fruiting bodies of this fungus were seldom encountered. For these reasons it is suspected that *S. chailletii* may be transmitted from tree to tree by bark beetles or sawyer beetles, possibly in the form of conidia or hyphal fragments.

Three fungi, the yeast, *O. bicolor*, and *Fungus F*, are evidently carried by insects from dead trees to the substrate of dying or very recently killed balsam fir. Assuming that the two remaining fungi, *S. chailletii* and *P. abietinus*, depend on air-borne spores for their spread and infection, they presumably could gain entrance to the substrate soon afterwards through the numerous openings in the bark resulting mainly from attacks by *P. sparsus* and, to a less extent, *M. scutellatus*.

Evidence has been presented elsewhere which indicates that holes formed by *M. scutellatus* larvae eventually do serve as entrances for *P. abietinus* spores, and that there is a relationship between the frequency of wood borer tunnels and the rate of development of sap rot caused by *P. abietinus* (6). Leach *et al.* (24) discovered a similar relationship in the development of sap rot caused by *Peniophora gigantea* (Fr.) Massee and the *Monochamus* population in felled Norway pine logs.

Factors Affecting Establishment and Activity in Dying and Dead Trees

The second and third hypotheses presented in the Introduction to explain the succession pattern of deterioration were: (*a*) competitive or synergistic interactions among the fungi, and (*b*) a dependence upon changes in certain properties of the wood substrate. Studies of the comparative growth rates and interactions of the fungi associated with the deterioration of balsam fir were undertaken to test the second hypothesis, and sections dealing with the effects of volatile and diffusible substances of balsam fir, substrate pH, and moisture content of wood upon the fungi are presented with regard to the third hypothesis. The data on fungus activity in relation to wood properties are treated comprehensively in the discussion.

Comparative Growth Rates and Interactions

The relative rates of spread through wood of several wood-inhabiting fungi do not necessarily correspond to their growth rates on malt agar. Similarly, the inhibitive or stimulative effects of the presence of one of these fungi upon the others in the wood substrate do not necessarily correspond to those displayed when the fungi are grown together on malt agar plates. The growth rates and interactions of the fungi on malt agar are easily determined, however, and provide an indication of the aggressiveness and competitiveness that might be expected of these fungi in the sapwood of dying and recently killed balsam fir.

Observations were made of the growth rates of *Ophiostoma bicolor*, *Fungus F*, *Stereum chailletii*, and *Polyporus abietinus* on malt agar plates by the following method: cubes of agar 3 mm square were removed from the advancing edges of vigorously growing cultures. These inocula were transferred aseptically to the edges of fresh sterile agar plates. The plates, each containing one inoculum, were stored at room temperature. Ten days later the average radius of five colonies of each fungus was as follows: *Fungus F* 83 mm, *O. bicolor* 61 mm, *S. chailletii* 32 mm, and *P. abietinus* 26 mm.

The same fungi were grown in pairs on malt agar plates to determine whether or not they exhibited any marked growth interactions. After observing that the growth rates of *O. bicolor* and *P. abietinus* were not inhibited when paired, no further tests of this pairing were made, since these two fungi were rarely found simultaneously in balsam fir wood. The other tests were repeated several times to confirm any observed differences in growth rates.

The growth rate of *O. bicolor* was not affected by the presence of *Fungus F*, although it was inhibited when approaching contact with *S. chailletii*.

Fungus F and *S. chailletii*, the two fungi isolated most consistently from red stain of balsam fir sapwood, exhibited some inhibition of growth shortly before contact was effected. The presence of *P. abietinus* had no visible effect upon the growth rates of these two fungi until the colonies had practically merged, at which point both colonies nearly stopped growing.

The growth rate of *P. abietinus* increased slightly when *Fungus F* or *S. chailletii* was present at a distance, but decreased sharply when it approached contact with *Fungus F*.

Hence, there is no evidence of marked inhibition or antagonism among the four fungi in culture, that is, no fungus was completely stopped and overrun by another. However, the behavior in culture in no way precludes the possibility that one might suppress another in balsam fir wood.

The Effects of Volatile and Diffusible Substances from Fresh Balsam Fir Wood

The growth of wood-rotting fungi may be stimulated by wood introduced into culture vessels, even if the wood is not in contact with the fungus or the medium (1). It was suggested that this stimulation of growth was due to the presence of a volatile substance given off by the wood. Tests were carried out to determine whether or not the volatile and diffusible substances of fresh balsam fir sapwood have any effect upon the growth rates of the four fungi under consideration and, if so, whether or not they favor the growth of particular fungi of the succession.

Fresh malt agar plates were inoculated at the edges with cubes of agar 3 mm square taken from the periphery of vigorous cultures of *Ophiostoma bicolor*, *Fungus F*, *Stereum chailletii*, or *Polyporus abietinus*. Sapwood shavings and sawdust from a healthy balsam fir were collected and placed in the bottom compartment of four desiccators. Four plates, containing cultures of each fungus, were placed in the upper compartment of the desiccators, and duplicate sets of plates were placed in the upper compartments of four otherwise empty desiccators.

Twelve chips, measuring roughly $\frac{3}{4}$ in. $\times$ $\frac{3}{4}$ in. $\times$ $\frac{1}{8}$ in., were cut from the sapwood of a healthy balsam fir. The chips were briefly surface-sterilized in 70% ethyl alcohol and placed in empty, sterile petri plates. Malt agar was then poured in the 12 plates so that the chips were completely submerged. Each of the plates was inoculated with one of the four fungi in the manner outlined above. Four plates, each containing a culture of a different fungus, were placed in the upper compartments of each of three otherwise empty desiccators.

The growth rates of the fungi in all 11 desiccators were checked periodically. In this way comparisons could be made of the growth rates of *O. bicolor*, *Fungus F*, *S. chailletii*, and *P. abietinus* when exposed to volatile or diffusible substances of balsam fir, and under normal laboratory conditions in which the same substances were absent. No significant differences could be detected in the growth rates of the fungi under these conditions, indicating that these substances do not significantly alter the growth rates of these fungi.

Substrate pH

Pronounced changes have been demonstrated in the pH of aqueous extracts of the sapwood of balsam fir in different phases and stages of deterioration. It has also been demonstrated that *Fungus F*, *Stereum chailletii*, and *Polyporus abietinus* are associated with different phases of sapwood deterioration (Table IV). An indication of the effect of the pH of the substrate on the vigor of the fungi was therefore necessary before any theory of

the mechanism of succession could be presented. This information was obtained by growing the fungi in media adjusted at different pH levels. A liquid rather than a solid medium was used, since actual mycelial weights provide more accurate measurements of growth than the diameters of colonies growing on a solid medium.

Cultures of *Fungus F*, *S. chailletii*, and *P. abietinus* were grown in media buffered at different pH levels. The basic formula of the medium was as follows:

5.0 g glucose
5.0 g asparagine
0.75 g $MgSO_4.7H_2O$
0.03 g thiamine hydrochloride
trace $FeCl_2$
1000 cc distilled water.

Different proportions of $M/3$ H_3PO_4, $M/3$ KH_2PO_4, and $M/3$ K_2HPO_4 were added to five aliquots of the basic medium so that media buffered at pH 3.0, 4.0, 5.0, 6.0, and 7.0 were obtained. Approximately equal amounts of phosphate were added to each aliquot.

Forty cubic centimeter portions of media were poured into 250 ml flasks, and these were autoclaved for 5 minutes at 15 pounds pressure. The pH values of the five media were then tested, and found to have been altered no more than 0.1 pH unit by this treatment.

Cubes of agar 3 mm square removed from the advancing edges of vigorous cultures of the three fungi were placed aseptically in the flasks so that six cultures of each fungus were started in each of the five buffered media. The flasks were stored at room temperature, and 3 weeks later a Buchner filter was used to filter the mycelia of the cultures on to pieces of filter paper that had previously been weighed to the nearest 0.1 mg. The oven-dry weights of the filter papers with adhering mycelia were then determined, and the increase in weight of the filter papers was used as a measure of the growth of the fungi during the 3-week period.

The pH of the filtrates were determined with a Beckman pH meter, and recorded. In only one instance was the pH of the media altered more than 0.1 pH unit during the course of the experiment; *Fungus F* was found to have lowered the pH of the media from 5.0 to 4.6.

In a repetition of this experiment, four aliquots of the media were buffered at pH 3.5, 4.5, 5.5, and 6.5.

The results of these experiments are illustrated in Fig. 17. The greatest growth of *P. abietinus* occurred in media adjusted at pH 4.5, whereas that of *Fungus F* and *S. chailletii* occurred in media adjusted at pH 6.5. Figure 17 also shows that these fungi, particularly *Fungus F* and *P. abietinus*, have very pronounced optima with regard to their growth rates in media adjusted at different pH levels.

Table III has shown that the pH of water extracts of the stained, firm sapwood of balsam fir in Phase 2 ranges from 5.0 to 6.3, whereas that of rotted

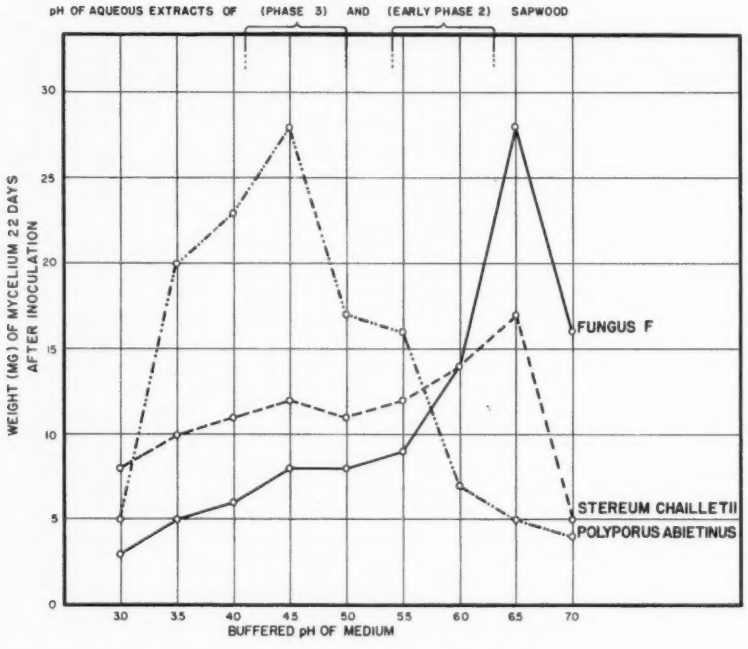


FIG. 17. The growth rates of *Fungus F*, *Stereum chailletii*, and *Polyporus abietinus* in liquid media buffered at different pH levels.

sapwood of balsam fir in Phase 3 ranges from 4.1 to 5.0. Table IV has shown that *Fungus F* and *S. chailletii* are mainly associated with Phase 2 and that *P. abietinus* is practically the only fungus associated with Phase 3. The brackets at the top of Fig. 17 show the ranges of the pH of aqueous extracts of balsam fir sapwood in two phases of deterioration. The pH during the early stages of Phase 2 is similar to that of liquid media which support the fastest growth of *Fungus F* and *S. chailletii*, whereas it is considerably higher than the optimum for the growth of *P. abietinus*. Towards the end of Phase 2, and at the commencement of Phase 3, the pH of aqueous extracts of the sapwood is lower (Table III), indicating that this wood may be more susceptible to *P. abietinus* invasion. Hence, there is a relationship between the pH of liquid media which supports the fastest growth of these three fungi, and the pH of balsam fir sapwood in those phases of deterioration with which each is associated.

Moisture Content of Wood

Tests of the effects of different moisture contents in balsam fir sapwood upon the development of the fungi associated with the deterioration of this species were not carried out. Table II has shown, however, that the average

moisture content of living balsam fir sapwood is approximately 145%, whereas that of sapwood in Phase 3 has been reduced to about 50%. Cartwright and Findlay (12) have concluded that moisture contents of between 35 and 50% in normal woods are the most favorable for the growth of wood-rotting fungi. The moisture content of the sapwood of trees in Phases 1 and 2 is generally higher than 50%, which is probably suitable for the development of the stain fungi, *Fungus F* and *S. chailletii* (25). However, this may inhibit the development of *P. abietinus* which might otherwise find the wood suitable for colonization. A more comprehensive treatment of the effect of wood moisture content on the development of these fungi is presented in the discussion.

Laboratory Studies of Decay and Fungal Interactions

Laboratory experiments were carried out to determine the significance of each of the three fungi that extensively invade the sapwood of dead balsam fir in the deterioration process, and to assess the effect of the establishment of one of these fungi in balsam fir sapwood upon the progress of the others. For these experiments, it was necessary to design a technique whereby wood sticks could be sterilized without drastic alteration, thus maintaining conditions as similar as possible to those in recently killed trees. The widely used autoclaving method of sterilization was therefore considered unsuitable. The alcohol immersion technique adopted for these studies has been described in detail in a previous contribution (5). Using sticks cut from the sapwood of living balsam fir, the proportion of parenchyma cells living at the end of this procedure was essentially the same as that in sound, healthy wood. There was, of course, no way of avoiding the earlier death of the tissues and other changes inherent in the isolation of portions of living trees. However, since *Fungus F*, *Stereum chailletii*, and *Polyporus abietinus* only attack dying or recently killed trees in nature, prolonged life of the cells would be abnormal and therefore detrimental in any studies of the effect of these fungi on balsam fir sapwood. The specially designed inoculation tube used in these studies has also already been described (5).

Changes in the Properties of Wood Infected in the Laboratory

To assess the significance of each of the three fungi that extensively invades the sapwood of dead balsam fir in the deterioration process, test sticks were inoculated with these fungi and subsequent changes in the properties of the sticks were examined. A record of these changes proved useful in subsequent studies as an indication of the progress of fungi in wood sticks previously infected with another fungus.

Ninety sticks from the sapwood of a single healthy balsam fir were sterilized and inoculated with *Fungus F*, *Stereum chailletii*, or *Polyporus abietinus*. An additional 30 sticks were sterilized and placed in tubes that contained no inoculum; these uninfected sticks are referred to as check sticks. Periodically, a number of sticks were removed and examined for some or all of the following properties: color, toughness, and pH of aqueous extracts.

The extent of decay of the test sticks was estimated from the reduction in their toughness. The more widely used method of determining ovendry weight losses was not attempted for reasons presented earlier; moreover, it was considered that subjecting the sticks to temperatures of 105° C before they were inoculated might alter them significantly.

Color

With inoculated sticks, changes in color occurred fairly rapidly after the mycelium had overrun the surfaces of the sticks, usually within 10 weeks of inoculation. Very little, if any, additional change in color occurred from that time until the last sticks were examined 23 weeks after the commencement of the experiment.

The average color notations of the four sets of test sticks examined in the later stages of the experiment are presented in Table V. This table also shows the color notations of healthy sapwood and sapwood in the different phases of deterioration which were described earlier.

The color of the check sticks was similar to that of healthy sapwood, and the color of sticks infected with *P. abietinus* was very nearly the same as that of rotted sapwood in Phase 3. This is not surprising, as *P. abietinus* was consistently isolated from sapwood in Phase 3.

TABLE V

Color notations of balsam fir sapwood in different phases of deterioration and of balsam fir sapwood sticks infected in vitro with *Fungus F*, *S. chailletii*, and *P. abietinus*

Sapwood of balsam fir trees		Test sticks infected in vitro	
Condition of sapwood	Color notation*	Inoculum	Color notation*
Healthy	2.5Y 8.5/4.5	Check sticks	2.3Y 8.1/4.8
Lightly stained	1.5Y 8.0/6.0	*Fungus F*	1.0Y 8.0/5.3
Deeply stained	9.0YR 7.0/7.25	*S. chailletii*	9.4YR 7.5/6.5
Rotted	8.5YR 6.75/9.0	*P. abietinus*	8.7YR 7.2/7.4

*Munsell system of color notation.

Test sticks inoculated with *S. chailletii* were stained a reddish color, which was almost as pronounced as that of deeply stained sapwood in the later stages of Phase 2. Test sticks inoculated with *Fungus F*, on the other hand, were stained even more faintly than lightly stained sapwood in the early stages of Phase 2. It has been pointed out that only *S. chailletii* and *Fungus F* were consistently isolated from both lightly and deeply stained sapwood of balsam fir trees in Phase 2. Hence, these observations indicate that *S. chailletii* is responsible for practically all of the medium to deep yellow-red discoloration of the sapwood of recently killed balsam fir, and, conversely, extensive sapwood discoloration in these trees indicates that *S. chailletii* is or has been active in that wood.

Toughness

By cutting all sticks from the sapwood approximately $\frac{1}{2}$ in. beneath the cambium, sticks composed of no less than six and no more than seven annual

rings were obtained. Differences in the toughness of test sticks due to differences in the spacing of the annual rings were therefore probably insignificant, and in any case were taken into account by the standard deviations which were computed for these data.

To reduce contamination, it was necessary to cut, sterilize, and inoculate wood sticks as rapidly as possible. For this reason only a limited number of sticks could be cut and treated in 1 day. Slight variations in the width of test sticks cut on different days were unavoidable, owing to limitations of the available machinery. Since variations in the toughness of these sticks would occur with variations in width, these differences were compensated for by having the sticks cut on 1 day uniformly distributed among the four inoculation treatments. Sticks selected for testing at one time were sticks that had been prepared on the same day.

Variations in width up to 0.05 mm were detected between infected test sticks cut on the same day. These slight variations were probably not significant, and were taken into account in the statistical treatment of the data. The width of the uninoculated check sticks, however, was found to be less than that of the infected sticks 8 weeks after inoculation, and this difference was greater at each succeeding test period. This was apparently due to the relatively fast rate of drying of check sticks. It is difficult to estimate the effect of shrinkage on the toughness of these sticks. A slight, progressive increase in the strength of coniferous wood specimens with successive stages of drying below the fiber saturation point has been demonstrated (28). For the purpose of this study it was assumed that the shrinkage of check sticks did not significantly alter their toughness.

The results of five series of tests of the toughness of infected and uninfected sticks are presented in Table VI, and are illustrated in Fig. 18. The tests were carried out 8, 13, 17, 20, and 23 weeks after the sticks had been cut and inoculated. Table VI shows no consistent difference during the course of the experiment between the toughness of the check sticks and of sticks infected with *Fungus F.* The toughness of sticks infected with *Stereum chailletii* or *Polyporus abietinus* for 13 or more weeks, on the other hand, was

TABLE VI

The toughness of balsam fir sapwood sticks infected with *Fungus F, S. chailletii,* and *P. abietinus*

Test run	Time elapsed following infection when tested, weeks	Average thickness of check sticks, mm	Average thickness of infected sticks, mm	Average energy (ft-lb) absorbed in breaking test sticks, toughness*			
				Check sticks	Inoculum		
					Fungus F	*S. chailletii*	*P. abietinus*
1	8	10.118	10.120	2.43 (3)	2.39 (3)	2.20† (3)	2.08† (3)
2	13	10.235	10.253	2.77 (3)	2.12† (6)	1.61‡ (4)	1.31‡ (4)
3	17	10.079	10.107	2.02 (3)	2.22 (6)	1.29‡ (5)	1.28‡ (3)
4	20	10.109	10.164	2.51 (3)	2.77 (4)	1.50‡ (5)	0.82‡ (4)
5	23	10.061	10.158	2.37 (3)	2.27 (3)	1.16‡ (3)	0.77‡ (3)

*The number of sticks tested in each case is shown in brackets.
†In comparing the toughness of infected and check sticks, the value of t lies between the 5% and 1% level of probability.
‡In comparing the toughness of infected and check sticks, the value of t is greater than the 1% level of probability, indicating that the difference in toughness of the two groups of sticks is significant.

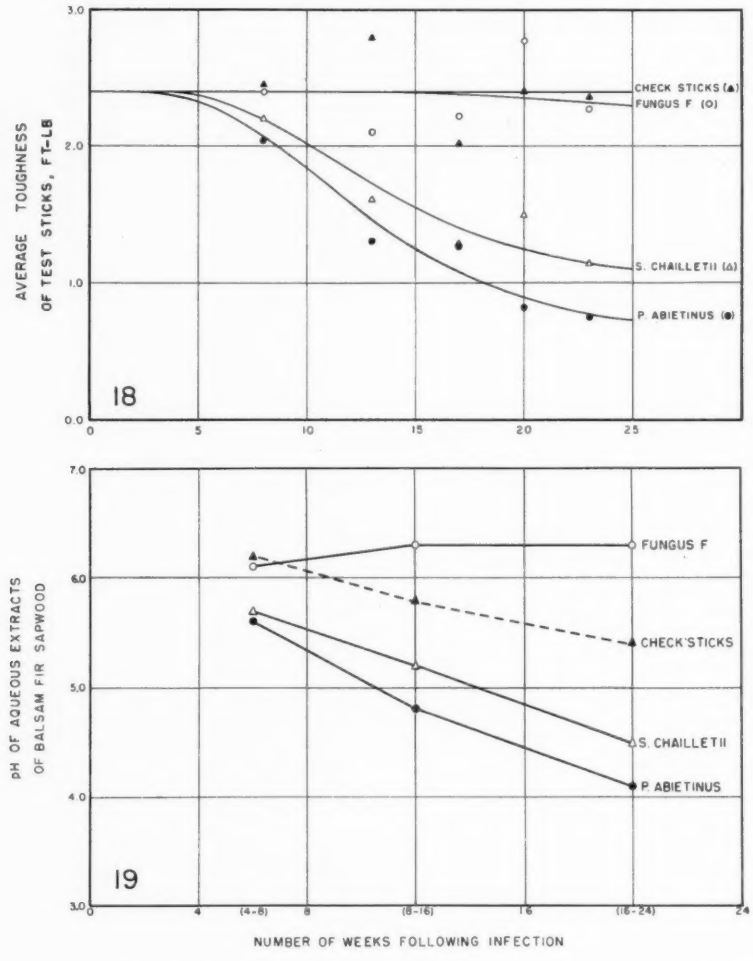


FIG. 18. The reduction in toughness of balsam fir test sticks infected with *Fungus F*, *Stereum chailletii*, and *Polyporus abietinus*.

FIG. 19. Changes in the pH of aqueous extracts of balsam fir sticks infected with *Fungus F*, *Stereum chailletii*, and *Polyporus abietinus*.

reduced significantly. Sticks infected with *P. abietinus* showed the greatest reductions in toughness in each series of tests; in tests carried out 20 and 23 weeks after inoculation the toughness of these sticks was only approximately 35% of that of uninfected sticks.

It has already been demonstrated that the first noticeable reduction in the toughness of test sticks cut from the sapwood of dead balsam fir in the field occurred in wood that was still "firm" but stained a pronounced reddish color. Tables V and VI show that test sticks infected with *Fungus F* were stained very faintly during the course of the experiments, and their toughness was not reduced significantly; and that test sticks infected with *S. chailletii* were markedly reddened at the end of the experimental period, their toughness being reduced significantly in only 13 weeks. This would indicate that the toughness of deeply stained balsam fir sapwood in nature is reduced because the wood has been infected with *S. chailletii* for some time. Lightly stained sapwood, on the other hand, may be presumed not to have been infected with *S. chailletii* long enough to affect the toughness appreciably. Table VI indicates that even prolonged activity by *Fungus F* would not reduce the toughness of balsam sapwood.

Histological studies of the sticks infected in the laboratory indicated, as suggested by Proctor (34), that the pronounced reductions in toughness due to *S. chailletii* and *P. abietinus* result from dissolution of the wood by enzymic activity. *S. chailletii* was observed to move from cell to cell only through pit apertures and membranes, and while holes were formed in the cell walls by *P. abietinus* the extremely small size of these (less than 2μ in diameter), and their very scattered distribution, suggest that the weakening effect of this fungus is not mainly due to the mechanical effect of the perforations.

pH

The pH of aqueous extracts of uninfected balsam fir sapwood sticks, and of sticks infected with *Fungus F*, *Stereum chailletii*, and *Polyporus abietinus*, was determined at intervals throughout this experiment. The results are presented in Table VII and Fig. 19. The pH of aqueous extracts of uninfected test sticks decreased slowly but progressively from 6.2 to 5.4 during

TABLE VII

The pH of aqueous extracts of balsam fir sapwood sticks infected with *Fungus F*, *S. chailletii*, and *P. abietinus*

Time elapsed following infection when tested, weeks	Average pH of aqueous extracts of test sticks*			
	Check sticks	Inoculum		
		Fungus F	*S. chailletii*	*P. abietinus*
0–8	6.2 (4)	6.1 (5)	5.7 (4)	5.6 (5)
8–16	5.8 (5)	6.3 (6)	5.2 (4)	4.8 (4)
16–24	5.4 (10)	6.3 (18)	4.5 (14)	4.1 (11)

*The number of sticks tested in each case is shown in brackets.

the experiment. The pH of the aqueous extracts of test sticks inoculated with *Fungus F*, on the other hand, remained almost constant, averaging between 6.1 and 6.3. Hence, the presence of *Fungus F* in balsam fir sapwood tends to prevent the drop in pH that occurs in uninfected wood.

The average pH of aqueous extracts of test sticks inoculated with *S. chailletii* was lower than that of the check sticks during the first 8 weeks after inoculation, and decreased at a greater rate throughout the remainder of the experiment. This indicates that *S. chailletii* had an acidifying effect upon balsam fir sapwood. The action of *P. abietinus* resulted in an even more pronounced increase in the acidity of balsam fir sapwood sticks in vitro than *S. chailletii* (Table VII).

The Effect of the Establishment of One Fungus in Wood Sticks upon the Progress of Another Fungus

Eighty-one sticks cut from the sapwood of a healthy balsam fir were sterilized and inoculated. Thirty of these were inoculated with *Fungus F*, 30 with *Stereum chailletii*, and 21 with *Polyporus abietinus*. An additional 30 sticks were sterilized and placed in tubes that contained no inoculum.

After 10 weeks, 16 of the inoculated sticks had become contaminated and were discarded. The remaining 65 were covered with mycelium, and, on the basis of similar experiments described earlier, judged to be well infected. These sticks were then removed from the inoculation tubes with sterilized forceps, and most of the superficial mycelium was scraped off with a sterilized scalpel. The remaining external mycelium was removed by rubbing each stick with a clean towel. The sticks were then immersed in 70% ethyl alcohol for approximately 20 seconds, removed and shaken gently in the air with sterilized forceps for about 10 seconds to remove excess alcohol, and placed in sterile inoculation tubes containing fresh, vigorously growing cultures of *Fungus F*, *S. chailletii*, or *P. abietinus*.

None of the 30 uninoculated sticks had been contaminated at this time. These check sticks were also removed from their "inoculation" tubes, immersed in 70% ethyl alcohol for approximately 20 seconds, removed, shaken, and placed in sterile inoculation tubes containing fresh cultures of the same three fungi.

The 95 transferred sticks were stored in their new tubes for an additional 10-week period. These two 10-week inoculation periods will be referred to as stage 1 and stage 2 of the experiment. Only six of the 95 sticks became contaminated during stage 2; these were discarded.

The test sticks are referred to in an abbreviated form based on the treatments they were subjected to during the two stages of the experiment. For example, sticks that were uninoculated (check sticks) for the first 10-week period and infected with *S. chailletii* during the second 10-week period are referred to as check – *S. chailletii* sticks, and the term *Fungus F* – *P. abietinus* sticks is used to refer to sticks infected with *Fungus F* during the first stage of the experiment and with *P. abietinus* during the second stage.

Visual Inspection

The superficial mycelia of *Fungus F*, *S. chailletii*, and *P. abietinus* growing on balsam fir test sticks were quite distinctive in appearance, and with very little experience could be recognized easily. *Fungus F* formed an even, downy to velvety mycelial mat, sometimes with brownish woolly areas; *S. chailletii* produced a thick, woolly, even mat; whereas sticks infected with *P. abietinus* were covered with a fairly thick, cottony mycelial mat with characteristic thick, scattered tufts. Hence, at the end of the 20-week, two-stage inoculation period, the identity of these mycelial mats could be determined readily, and the relative densities of the mats could be estimated.

Ocular examinations indicated that balsam fir test sticks that had been infected with *S. chailletii* were not attacked by *Fungus F* as extensively or as rapidly as were uninoculated sticks; and that test sticks previously infected with *Fungus F* were, to a certain degree, protected against an attack by *S. chailletii*. It also appeared as though test sticks infected with *Fungus F* or with *S. chailletii* were afforded a much greater degree of protection than uninfected sticks against the invasion and establishment of *P. abietinus*. However, microscopic examinations and descriptions of the changes that take place in three of the properties of these sticks, which are discussed below, showed clearly that visual inspection is not a reliable method of determining the extent to which secondary fungi have invaded and deteriorated sticks previously infected with another fungus.

Histological Examination

Thin sections suitable for microscopic examination were cut from two test sticks of each group that had been subjected to the same inoculation procedure. In the two *P. abietinus* – *Fungus F* sticks, *Fungus F* was found growing in the wood cells, but it was relatively scarce. Examinations of check – *P. abietinus* and *Fungus F* – *P. abietinus* sticks revealed that *P. abietinus* hyphae were abundant in the central portions of the sticks, near the inoculum source, but were relatively scarce at both ends. The scarcity of *P. abietinus* hyphae near the ends of the latter sticks was particularly striking. In all of the other sticks examined microscopically, the fungus which served as the inoculum for the second stage of the experiment was observed growing extensively in the wood cells throughout the sticks.

Color, pH, and Toughness

Table VIII presents, for each of the 12 inoculation procedures, the average color notation of test stick shavings, the average pH of aqueous extracts of test sticks, and the average toughness of the test sticks. All of these measurements were taken at the end of the 20-week inoculating period. The figures for these three properties, color, pH, and toughness, can be compared with those obtained in similar tests carried out on check sticks and on sticks infected with a single fungus, presented in Tables V, VII, and VI, respectively.

Three days were needed to prepare all of the test sticks required for this experiment. It has been pointed out that slight, unavoidable variations

TABLE VIII

The color, pH of aqueous extracts, and toughness of balsam fir sapwood sticks after two successive 10-week inoculation periods

Condition of sticks after the first 10-week period	Average color of test sticks* Inoculum for the second 10-week period			Average pH of aqueous extracts of test sticks† Inoculum for the second 10-week period			Average toughness of test sticks‡ Inoculum for the second 10-week period		
	Fungus F	*S. chailletii*	*P. abietinus*	*Fungus F*	*S. chailletii*	*P. abietinus*	*Fungus F*	*S. chailletii*	*P. abietinus*
Uninoculated check sticks	2.0Y 8.2/5.5	1.0Y 8.0/5.5	1.0Y 8.0/5.5	6.0 (10)	5.7 (10)	5.7 (8)	2.25	1.98	1.84
Infected with *Fungus F*	1.0Y 8.0/6.0	1.0Y 8.0/5.5	0.5Y 7.8/5.8	6.2 (8)	6.1 (7)	5.9 (8)	2.29	1.77	1.71
Infected with *S. chailletii*	9.5YR 7.5/6.5	9.5YR 7.5/7.0	9.5YR 7.5/6.5	5.0 (7)	4.8 (8)	4.8 (8)	1.85	1.69	1.23
Infected with *P. abietinus*	9.0YR 7.5/7.0	9.0YR 7.2/7.5	8.5YR 7.0/7.5	4.6 (5)	4.5 (5)	4.5 (5)	1.44	1.61	1.01

*Munsell system of color notation.
†The number of sticks tested in each case is shown in brackets. All of these sticks were tested for the three properties included in this table.
‡Figures represent average ft-lb absorbed in breaking test sticks.

occur in the dimensions of test sticks cut on different days. To overcome this source of error in the toughness tests, sticks prepared on the same day were distributed uniformly among the 12 inoculation procedures.

Analysis of Results

In the section of this paper dealing with the occurrence of the fungi in dying and dead trees, it was pointed out that *Fungus F* and *S. chailletii* apparently invade the sapwood of balsam fir soon after the death of the host, and that *P. abietinus* does not become established until almost a year later, at which time the sapwood is thoroughly infected with the former two fungi. The main objective of these succession studies was to determine what effect the prior establishment of *Fungus F* in balsam fir had upon S. *chailletii*, and vice versa; and to assess the effect of these two fungi upon the subsequent progress of infection of *P. abietinus*. Five criteria were used to judge the progress of infection of the secondary fungi. These were visual inspection, microscopic examination, and changes in the toughness, pH of aqueous extracts, and color of test sticks. Microscopic examination and changes in toughness are considered to be more reliable in determining the progress and deteriorating effects of the fungi than the other three criteria.

Although *S. chailletii* invaded *Fungus F – S. chailletii* sticks quite extensively, *Fungus F* formed most of the superficial mycelium on the sticks. The presence of *Fungus F* inhibited the characteristic tendency for *S. chailletii* to reduce the pH of aqueous extracts of balsam fir wood. However, *S. chailletii* was capable of reducing the toughness of sticks previously infected with *Fungus F* to a significantly greater degree than that of previously uninoculated sticks (4). Hence, the presence of *Fungus F* in balsam fir sapwood sticks does not inhibit, and may even promote, the establishment and deteriorating capacity of *S. chailletii*.

It is difficult to estimate the effect of the presence of one fungus upon the progress of *Fungus F*, as the effects of this fungus acting alone on balsam fir wood were either relatively minor or negative, that is, a slight increase in pH, a very faint discoloration, and no reduction in toughness. *Fungus F* extensively invaded *S. chailletii – Fungus F* sticks, and formed superficial mycelium apparently at the expense of *S. chailletii*. During the second phase of the experiment, when *Fungus F* was substituted for *S. chailletii* as the source of inoculum, further changes in the color, toughness, and pH of the sticks occurred. These changes were probably due to the continued action of *S. chailletii*. Since these changes occurred at a slower rate in these sticks than in *S. chailletii – S. chailletii* sticks during stage 2 of the experiment, *Fungus F* may have suppressed the action of *S. chailletii*. However, the explanation for this may be simply that the source of *S. chailletii* inoculum was removed from *S. chailletii – Fungus F* sticks at the end of the first stage of the experiment.

To sum up, there is no evidence that *Fungus F* and *S. chailletii* are strongly inhibited by, or antagonistic towards, each other in balsam fir wood. There are indications that, if anything, they may be mutually beneficial.

P. abietinus invaded *S. chailletii* – *P. abietinus* sticks extensively, but most, if not all, of the superficial mycelium on the sticks was *S. chailletii*. The determination of the extent to which *P. abietinus* altered the three properties of the sticks included in Table VIII is complicated by the fact that the individual action of this fungus and of *S. chailletii* had similar effects on these properties, the only difference being that the changes associated with *P. abietinus* over a given period were, as a rule, slightly more extensive (Tables V, VI, and VII). Table VIII shows that the average amount of energy absorbed in breaking *S. chailletii* – *P. abietinus* sticks was 1.23 ft-lb, compared with an average of 1.69 ft-lb in breaking *S. chailletii* – *S. chailletii* sticks. The fact that this difference in the toughness of these two types of sticks is significant at the 1% level of probability (4) indicates that the progress of *P. abietinus* in balsam fir sapwood is probably not inhibited, and may even be favored, by prior infection with *S. chailletii*.

P. abietinus extensively invaded the central two thirds of *Fungus F* – *P. abietinus* sticks, but was slow in colonizing the ends; and *Fungus F* formed all of the superficial mycelium on the sticks. Table VIII indicates that, during the second phase of the experiment, *P. abietinus* was not capable of appreciably staining or lowering the pH of sticks previously infected with *Fungus F*. *Fungus F* – *P. abietinus* sticks were stained red in the lower-central regions, however, and it is assumed that had these areas been large enough to test, they would have yielded an average pH of aqueous extract considerably lower than 5.9, as well as a color notation much closer to the typical red stain associated with the activity of *P. abietinus*. The average amount of energy absorbed in breaking *Fungus F* – *P. abietinus* sticks was 1.71 ft-lb, compared with an average of 1.84 ft-lb in breaking check – *P. abietinus* sticks. This difference in toughness is not significant (4), but it does indicate that, although prior infection of balsam fir sapwood with *Fungus F* may have a slight inhibitory effect on the spread of *P. abietinus*, it does not affect the deteriorating capacity of the latter once it becomes established in the wood.

Discussion and Summary

Decays, including deterioration, of the trunks of trees are diseases which develop slowly when compared with those of softer and more succulent tissues, such as leaves or parts of herbaceous plants. It might be expected, therefore, that more than one fungus could be involved during the course of decay, and evidence is accumulating that successions and interactions may be the rule rather than the exception in such diseases.

The fungi involved in the deterioration of the sapwood of most tree species fall into two distinct groups, both taxonomically and according to the type of deterioration with which they are associated. The fungi which are first encountered are usually responsible for sap stains, and belong mainly to the group Fungi Imperfecti; these organisms are dependent upon a relatively high moisture content of the wood and upon the cell sap for nourishment (25). These fungi are generally followed by basidiomycetes which are capable

of rotting the sapwood. There exists a controversy concerning the effects of these sap-staining fungi upon the initiation and progress of infection of the wood-rotting fungi which follow them. Björkman (9) refers to the opinion of Falck (16) and Wehmer (cf. Mez (29)) that "*Merulius* spores could only with great difficulty germinate in and attack green wood, if the wood had not previously been acidified through the attacks of e.g. mould fungi." Björkman also reported that, "According to Mayer-Wegelin, Brunn, and Loos (1931) who investigated green wood, the occurrence of advanced blue stain constitutes on the contrary an effective protection against decay, even though the infection of decay producing fungi may not be prevented" (27). Both von Johann, in 1931 (23), and Björkman, in 1947 (9), basing their results only on ocular examination of sticks and the development of hyphae, concluded that blocks of wood infected with species of *Ophiostoma* were in this manner given a degree of protection against subsequent attack by rotting fungi. Findlay, in 1939 (17), reported that the rate of decay of stained pine sapwood, as measured by losses in dry weight, was slightly greater than that of unstained wood, although the differences were not of any practical significance. In his book entitled Principles of Plant Infection (20), Gäumann stated, ". . . . the initial rots thus prepare the way for the destructive rots to colonize the healthy wood which they cannot attack unaided."

The mechanisms of these fungal successions in the deterioration of trees are of considerable practical and theoretical interest. The present study has provided sufficient data for at least a tentative proposal concerning these mechanisms with regard to the succession involved in the deterioration of balsam fir killed following extensive spruce budworm defoliation.

The trunk of each dying or killed balsam fir may be considered as a separate ecological unit. Depending on the moisture condition of the underlying ground, the average moisture content of the trunks of shallow-rooted trees that are blown down soon after death may be higher or lower than that of the trunks of dead standing trees. Further differences are likely to occur in trees in which one side has died before the other. However, most of the killed balsam fir in the two regions studied appeared to die uniformly on all sides, and remained standing for at least five years after death. Furthermore, it is assumed, or has been demonstrated, that any other variations in the environmental factors in different trees either are minor ones, or do not significantly affect the deterioration process. Hence, environmental factors that influence the activity of the fungi which are associated with the deterioration of these trees are approximately uniform.

Three hypotheses have been presented to explain the succession of the five fungi prominently involved in the deterioration of balsam fir. The first is the ability of the preliminary fungi to reach the substrate before the others. The automatic transmission of the yeast, *Ophiostoma bicolor*, *Fungus F*, and possibly *Stereum chailletii* by insects into dying and recently killed trees may permit these fungi to reach the substrate a few days, or at least a few hours, before air-borne spores of *Polyporus abietinus* (and possibly *S. chailletii*)

enter through the insect holes in the bark. However, this advantage is clearly not sufficient to explain the predominance of the yeast and *O. bicolor* during the first month of deterioration, or the delay of almost one year in the establishment of *P. abietinus*.

The second hypothesis advanced to explain succession is competitive or synergistic interactions among the fungi. There was no evidence of marked inhibition or antagonism among the four fungi tested in culture, and the general conclusion arrived at from succession tests was that the presence in balsam fir sapwood of one of the fungi that extensively invade dead trees has very little effect upon the subsequent infection and deteriorating capacity of the others.

Evidence from this investigation suggests that the principal explanation for the succession pattern of fungi in the deterioration of balsam fir lies mainly in the third hypothesis, which postulates that there is a dependence upon changes in certain properties of the wood substrate. It can be argued that since some of these changes may be directly or indirectly due to the presence of preliminary fungi, the second hypothesis cannot be discounted entirely. Indeed, the succession experiments may be regarded as indicating whether or not changes occur in infected test sticks which favor or retard the establishment of succeeding fungi.

It is postulated, then, that one or more changes that occur in the wood substrate during the 18-month period that includes 1 month before and 17 months after apparent tree death account for the succession pattern of deteriorating fungi. In this respect at least five changes must be considered, namely, (*a*) temperature, (*b*) chemistry of the wood, (*c*) hydrogen-ion concentration, (*d*) the change in wood from a "living" to a "dead" state, and (*e*) moisture content.

In earlier studies the author observed that the season of death of balsam fir had no noticeable effect upon the general succession pattern of deteriorating fungi (3, 6). Hence, it does not seem likely that temperature variations critically affect this pattern.

Changes in the chemical composition of balsam fir sapwood during and following death have not been considered thoroughly in this study. However, since in the laboratory *P. abietinus* was capable of infecting sapwood recently cut from living balsam fir, it is unlikely that the absence of this fungus in the sapwood of trees that have been dead for less than one year can be ascribed to a lack of essential nutrients in that wood.

The pH of balsam fir cambium and sapwood decreased as deterioration progressed (Table III). This was regarded as a possible explanation for the delay of approximately one year in the establishment of *P. abietinus* in the sapwood of dead balsam fir. Variations in the growth rate of *P. abietinus* due to differences in the pH of two substrates as dissimilar as an artificial liquid medium and balsam fir sapwood do not necessarily correspond; nevertheless, experimental results indicate that *Fungus F* might inhibit the colonization of balsam fir sapwood by *P. abietinus* through the capacity of the

former organism to maintain the pH of the wood at a higher level than is favorable for the establishment of *P. abietinus*. In nature, however, the sapwood of recently killed trees generally had a much lower pH than sticks infected with *Fungus F*, perhaps because of the presence of *S. chailletii*. Furthermore, balsam fir sticks with relatively high aqueous extract pH values were infected in the laboratory with *P. abietinus* mycelium. Hence, the pH of the sapwood of recently killed trees would apparently permit the the growth of *P. abietinus* mycelium.

The pH of the substrate may nevertheless account for the delay in the establishment of *P. abietinus* through its effect upon the many spores of this fungus which probably contact the sapwood of recently killed balsam fir through the numerous insect holes in the bark. It is possible that *P. abietinus* spores cannot germinate on such sapwood until it has become modified in some way, perhaps acidified; the spores of wood-destroying fungi generally require acid conditions for germination, and are slow to germinate even on optimal media. An investigation of the germination requirements of *P. abietinus* spores may elucidate this question.

It has been established that the moisture content of balsam fir sapwood decreased quite strikingly as deterioration progressed (Table II). The findings of this investigation and the foregoing discussion strongly suggest that this factor is of paramount importance in regulating the succession of fungi involved in the deterioration of balsam fir. Although the five principal fungi apparently reach the cambium and outer xylem of dying trees at approximately the same time, *Fungus F* and *S. chailletii* were seldom isolated before trees had been dead for about one month. It is postulated that *O. bicolor* and the yeast, which were frequently isolated from dying and very recently killed trees, are capable of invading very moist balsam fir tissues or tissues that contain living or very recently killed cells, whereas *Fungus F* and *S. chailletii* are not. It seems likely that both of these substrate changes are associated with this sequence of fungi.

The delay of almost one year in the establishment of *P. abietinus* could be quite conceivably a question of moisture content of the sapwood. Test sticks from the sapwood of healthy balsam fir were infected in the laboratory with *P. abietinus* mycelium within four or five weeks, but the moisture contents of these sticks averaged only 35% at that time. Nearly all of the samples of balsam fir sapwood tested within one year after tree death, in Phase 2 of deterioration, had moisture contents of between 60 and 80%. Moisture contents of between 35 and 50% in normal woods are considered to be most favorable for the growth of wood-rotting fungi (12). These facts suggest that *P. abietinus* was seldom isolated from the sapwood of balsam fir that had been dead for less than one year because the moisture content of this wood was still too high for the establishment of this fungus. The moisture content requirements and limitations for the establishment and growth of *P. abietinus* in balsam fir sapwood would appear to be a problem worthy of careful investigation.

The pathological deterioration process in killed balsam fir can be summarized briefly as follows. The tissues of dying balsam fir are first invaded by *O. bicolor* and the yeast, followed about one month later by *Fungus F* and *S. chailletii* when the trees have died, although all four fungi apparently may reach the substrate at approximately the same time. The reason for this sequence appears to be the inability of the latter two fungi to infect very moist balsam fir tissues, or tissues that contain living or very recently killed cells. *Fungus F* and *S. chailletii* extensively colonize most of the sapwood of the trees, as a rule, and *P. abietinus* is not encountered until approximately one year after tree death. Two explanations for the delay in the establishment of *P. abietinus* in the sapwood of these trees have been proposed. These are: (*a*) the inability of *P. abietinus* spores to germinate on the sapwood of recently killed trees, possibly because of the relatively high pH of the substrate; and (*b*) the moisture content of the sapwood of trees that have been dead for less than one year is too high for the establishment of *P. abietinus*.

In this study it has been necessary to consider critically the role of laboratory tests in evaluating field phenomena with regard to tree decays and deterioration. There is good evidence that determinations of the rate of decay of wood blocks from measurements of their ovendry weight losses, or after severe sterilization procedures such as autoclaving, are of questionable value since certain properties of the blocks or sticks are altered to a considerable but unknown extent. The fact that living parenchyma cells of test sticks were not killed by the technique used in this study indicates that this method permits laboratory tests to be undertaken under conditions which are much more closely related to actual field conditions than the other more widely used techniques, although precautions in interpretations are still necessary. Scheffer (36), in 1936, used a somewhat similar method although the cells of his test sticks were presumably killed; his procedures perhaps have not been adopted to the extent that their success and promise warranted. The success which has been obtained in the artificial inoculation of balsam fir sapwood with fungi that deteriorate this species in nature suggests that similar techniques may be used profitably in laboratory studies of the effects of other fungi causing heart rot and deterioration in their respective hosts.

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NOTES

A COMPARISON OF LOWER AND HIGHER PLANTS AS ACCUMULATORS OF RADIOACTIVE FALL-OUT[1]

EVILLE GORHAM

In an earlier paper (1) accumulation of radioactive fall-out by plants in the English Lake District was related to the mineral content of the various species, with both mosses and angiosperms low in mineral ash showing much more radioactivity than plants of high mineral content in the same groups. The present study compares radioactivity of ash from lichens, mosses, and angiosperms, using some of the data previously employed, plus counts for three lichens made toward the end of the work already reported.

The plants were collected in early 1958. Samples were dried at 105 to 110° C and ashed at bright-red heat. Aliquots of about 50 mg ash were fixed in planchets with "Celloidin" and tested within three days of collection for radioactivity, in a lead tower with CV 2139 counter tube (end-window weight 2.3 mg/cm^2). At least 1000 counts were recorded for each sample on a "Panax 44A" scaler. Background counts, averaging 8 per minute, were measured daily and subtracted from those shown in Table I and Fig. 1.

TABLE I

Radioactivity in angiosperms, mosses, and lichens of comparable ash content

Number of samples	Type of plant	Log % ash ± S.E.	Log c.p.m.* ± S.E.	Antilog % ash	Antilog c.p.m.*
10	Angiosperms	0.6606 ±0.0652	1.800 ±0.154	4.58	63
20	Mosses	0.6619 ±0.0493	2.183 ±0.092	4.59	152
3	Lichens	0.6536 ±0.1024	2.263 ±0.168	4.50	183

*Counts per minute for 50 mg ash.

No correction for self-absorption was applied, nor were the isotopes involved identified; so that the results merely give an arbitrary comparison of total activity under standard conditions. To give some crude comparison with a radioactive standard, counts were made of weights of potassium iodide similar to the weights of plant ash used. This salt contains about the same percentage of potassium as many plant ashes, and 50 mg yielded an average count rate of about 4 per minute, after subtraction of the background rate.

Table I summarizes the data for the various types of plant. In calculating the average values a logarithmic transformation was employed in order to

[1]This work was carried out while the author was on the staff of the Freshwater Biological Association, Ambleside, England.

bring the frequency distributions closer to the normal; and it will also be noticed that the ash contents of the three groups of plants were selected to be closely similar, thus minimizing the influence of ash content on count rate and emphasizing the effect of plant type.

A considerable difference is apparent in the radioactivity of the lower and higher plants, with the angiosperms exhibiting a mean (antilog) count rate of only 63 per minute in comparison with mean (antilog) rates of 152 and 183 for the mosses and lichens respectively. The difference between the log means for angiosperms and mosses is significant at the 5% level, that between mosses and lichens is quite insignificant. Separation of the 20 moss samples into species of woodland or semi-aquatic fen habitats, or into *Sphagnum* and other species, reveals little difference between these categories. The absence of any marked difference between the count rates of terrestrial woodland and semi-aquatic fen mosses suggests that fall-out is strongly held by the vegetation and not leached extensively from the wooded slopes into the wet and peaty valley bottoms. In this connection it may be noted that the plant ashes exhibited 23 times the radioactivity of ashes from evaporated stream waters (1).

Although no conclusive explanation for the greater radioactivity of the lower plants can be offered at this time, it may be presumed that they have a greater surface area per unit dry weight of tissue, and this should aid them not only in trapping particulate fall-out but also in absorbing the components soluble in surface runoff. Their habits of growth, as mats or cushions on the soil surface, should also enhance their ability to accumulate fall-out materials from runoff (cf. 3).

The decay of the radioactivity in these plants is illustrated in Fig. 1, where count rates of a sample of *Sphagnum papillosum* ash are plotted on a logarithmic scale against time. The curvilinear relationship is evidence that a mixture of

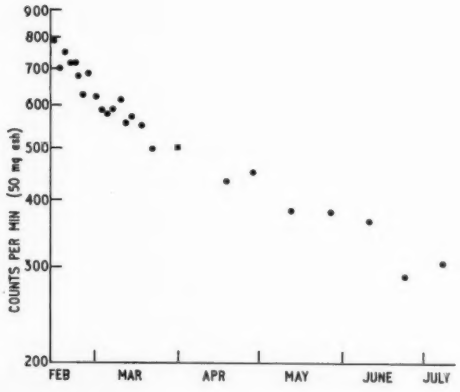

FIG. 1. Decay of radioactivity in a sample of *Sphagnum papillosum* ash.

isotopes is involved, while the relatively rapid decay points to fall-out from thermonuclear explosions as their source. Although the accident at the Windscale plutonium factory took place in October 1957 not far from the area in which the present study was made, it does not appear to have been responsible for the high radioactivity of the Lake District vegetation, since *Sphagnum papillosum* samples collected as far away as North Wales and northwest Scotland yielded count rates just as high as those collected within a few miles of the Windscale factory.

The chief practical conclusion to be drawn from this work is that animals feeding on mosses and lichens may well exhibit high intakes of radioactive fall-out on this account. In this connection a few reindeer bones from Norway have been shown to contain markedly greater concentrations of radioactive strontium-90 than sheep bones from the same country (2).

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